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Prof. M. A. B. Brazier[†]
Prof. M. Eden
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A. SPONTANEOUS ACTIVITY OF SINGLE UNITS IN THE COCHLEAR NUCLEUS

Single units in the nervous system frequently exhibit spikelike discharges in the absense of any controllable stimulation presented externally to the organism. The nature of these "spontaneous" discharges suggests that statistical descriptions might well reveal some basic properties of the units.

In recent studies[1] of the cochlear nucleus we have encountered many types of spontaneous discharge patterns. Some examples of these patterns are shown in Fig. XVIII-1. Each trace shows a series of spikelike deflections that represents the all-or-none discharges of a different single unit. Obviously there are some gross differences in the time patterns of the spikes. Unit 261-1 seems to fire in bursts; unit R-4-10 seems to fire almost regularly with no very long intervals between spikes; units 259-2 and 240-1 show irregular patterns of firing at different average rates.

Figure XVIII-2 shows interspike interval histograms[2] for the same data from which Fig. XVIII-1 was chosen. The histogram for unit 259-2 appears to be unimodal and asymmetric with an exponential tail. The histogram for unit R-4-10 appears to be unimodal and symmetric. Further analysis shows that this histogram is fitted rather indifferently by a Gaussian distribution. The histogram for unit 261 is bimodal and asymmetric. The histogram for unit 240-1 is unimodal, asymmetric, and has a tail

UNIT 259-2

UNIT R-4-10

UNIT 261-1

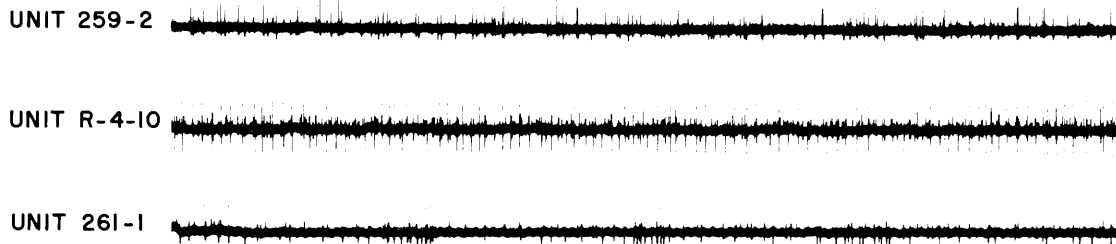Fig. XVIII-1. Film strips of the spontaneous activity of four selected units.
Upward deflections indicate negativity of the microelectrode
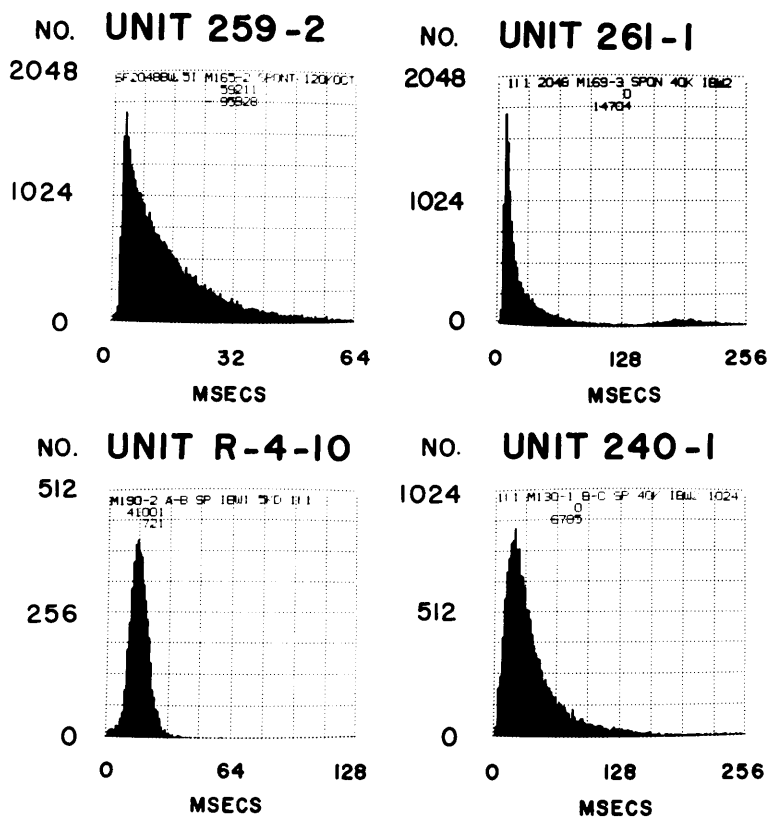relative to the headholder.

Fig. XVIII-2. Interval histograms for the spontaneous activity of the four units
shown in Fig. XVIII-3. The number N of intervals processed:
Unit 259-2, N = 40,960; Unit R-4-10, N = 5000; Unit 261-1, N =
16,384; Unit 240-1, N = 16,384.

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that decays more slowly than does an exponential curve.

Figure XVIII-3 shows joint interval histograms[3] for the same units. If we examine the cluster at the upper left and the one at the lower right we see that there is a tendency for a long interval (approximately 200 msec) to be preceded by a short interval (approximately 8 msec) and to be followed by a medium interval (approximately 30-60 msec). Further analysis of the joint interval histograms for the remaining three units shows that these units exhibit less correlation between successive intervals. For unit 240-1 there is a strong positive correlation between successive intervals for intervals of less than 30 msec, but rather little correlation for longer intervals. Unit R-4-10 shows a very weak positive correlation between successive intervals. In the mean, short intervals tend somewhat to be followed by short intervals, and long intervals by long intervals. Finally, unit 259-2 shows linear independence of successive intervals.

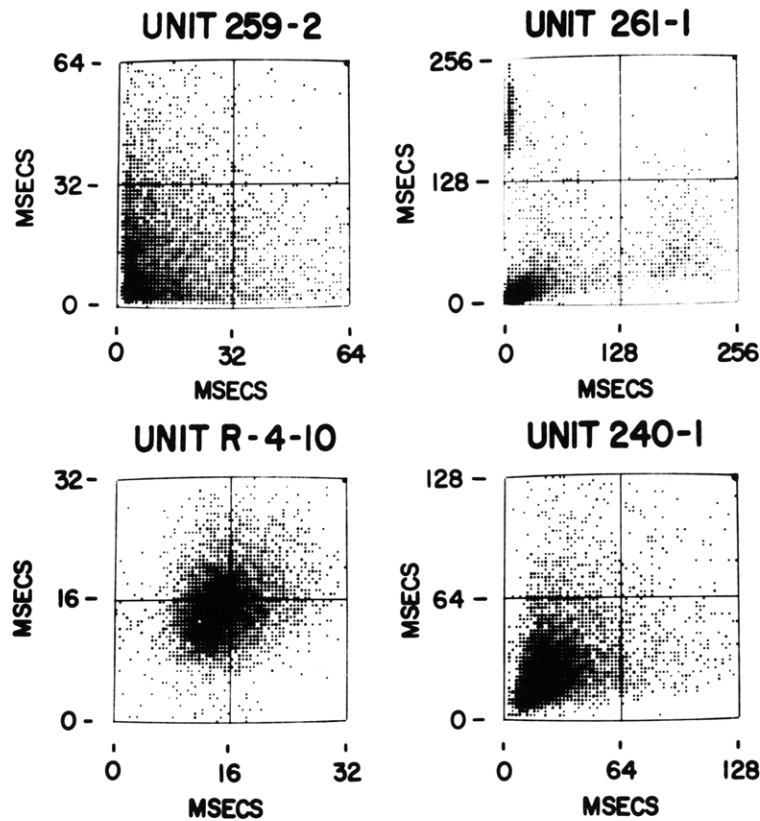The information given in this report suggests descriptive models for the spontaneous

Fig. XVIII-3. Joint interval histograms for the four selected units. The abscissa represents τ_1, the first of each ordered pair of intervals, the ordinate represents τ_2, the second of each ordered pair of intervals. The number of interval pairs processed for each unit was 4096.

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discharge patterns of the several units. For example, measurements on unit R-4-10 suggest a basically periodic process with an uncorrelated, quasi-Gaussian time jitter. By contrast, for unit 259-2, the exponential tail, the absence of very short intervals, and the linear independence of successive intervals suggest a Poisson-like process with a dead time.

There are some indications that discharges occurring in bursts, such as for unit 261-1, may be correlated with injury. Additional measurements on the spike train of unit 240-1 are needed in order to suggest a model.

R. W. Rodieck, N. Y-S. Kiang, G. L. Gerstein

References

1. N. Y-S. Kiang, A category of cells in the cat's cochlear nucleus defined by electrophysiological experiments, Quarterly Progress Report No. 61, Research Laboratory of Electronics, M.I.T., April 15, 1961, pp. 179-183.

2. G. L. Gerstein and N. Y-S. Kiang, An approach to the quantitative analysis of electrophysiological data from single neurons, Biophys. J. 1, 15-28 (1960).

3. G. L. Gerstein, Joint probabilities in firing patterns of a single neuron, Quarterly Progress Report No. 63, Research Laboratory of Electronics, M.I.T., October 15, 1961, pp. 176-180.

B. THE EFFECTS OF BACKGROUND NOISE ON EVOKED CORTICAL RESPONSES IN UNANESTHETIZED CATS

Previously we described[1] certain characteristics of the evoked response complex (ERC) recorded with gross electrodes implanted over the auditory cortex of cats. We have demonstrated that various components of the ERC behaved differently as the "state" of the animal changed. In the averaged response, the ER_1 (see Fig. XVIII-4), a surface-positive deflection with a peak latency of 8-12 msec, remained essentially unchanged after prolonged exposure to acoustic clicks or after injections of Nembutal anaesthesia. In contrast, a later, longer-lasting surface-negative component with a peak latency of 60-80 msec was markedly reduced after prolonged exposure to the clicks or after administration of Nembutal. The fact that the ER_1 precedes the later negative component suggests the possibility that the negative component is dependent upon the presence of the ER_1. Data that bear on this question have recently been obtained from experiments in which acoustic clicks are presented in a background of noise.

The recording procedure was similar to that reported previously.[1] All responses shown in Figs. XVIII-4 and XVIII-5 were taken while the animal was awake. Clicks at a constant rate and intensity were delivered into the room by a loud-speaker. Continuous background noise was then presented at several intensities. The responses from the cortex were averaged by the ARC-1 computer. The averaged responses to clicks alone

CC7

LATE
NEGATIVE

CLICK ALONE

CLICK PLUS NOISE

ER₁

25 μv

40 MSEC

CC 10

ER₁   LATE
NEGATIVE
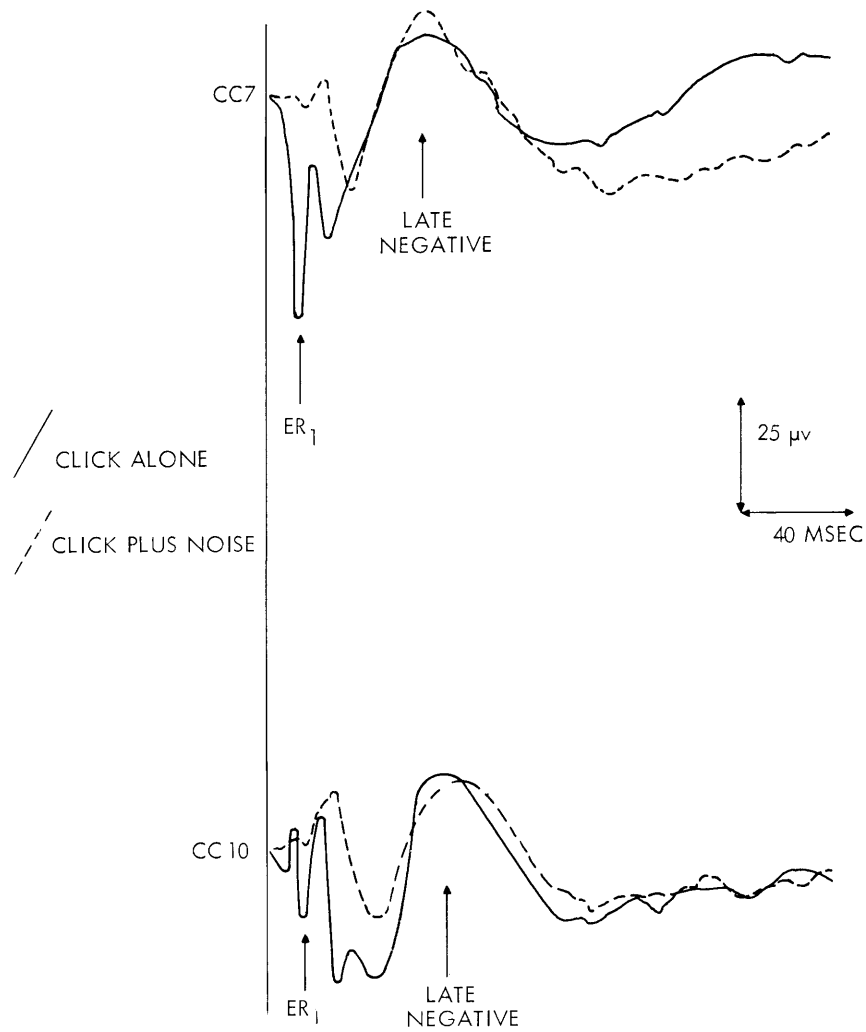
Fig. XVIII-4. Averaged evoked responses to clicks taken from two awake
cats (CC 7 and CC 10) with and without background noise. Solid
traces, clicks alone; dotted traces, clicks in the presence of
noise. The intensity level of the clicks is approximately 50 db re
detection level of the averaged responses. Number of responses
averaged, 64. For this figure noise intensities were chosen so
that the ER_1 was reduced substantially, while the later negative
component was not.

Fig. XVIII-5. Peak magnitudes of ER_1 and the late negative components, expressed as percentages of the magnitudes of the response to the click alone, plotted for a number of background noise 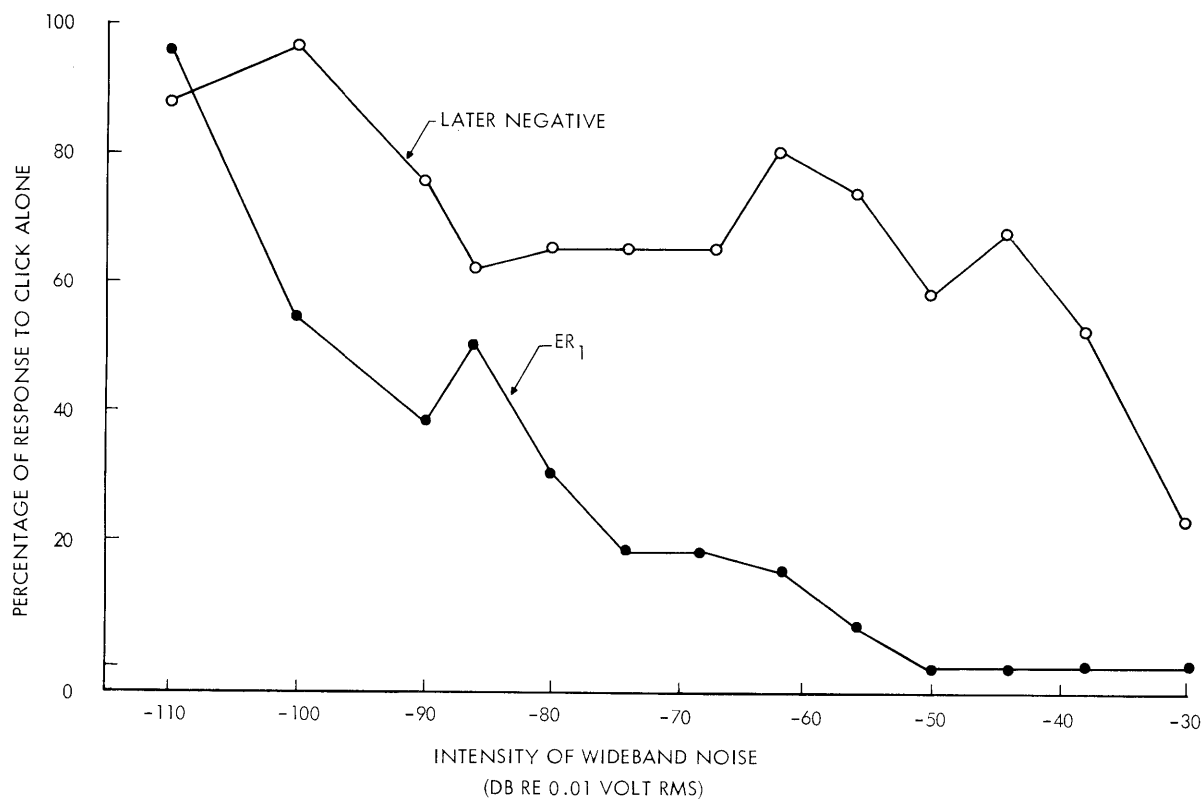levels. The decrease in magnitude of ER_1 is greater than that of the late negative component for a wide range of noise levels.

are shown in Fig. XVIII-4 (solid traces). With background noise the ER_1 is markedly reduced in amplitude, while the negative component remains relatively unchanged (dotted traces).

That this differentiation by background noise is only effective over a certain range of noise levels is shown in Fig. XVIII-5 in which the amplitudes of the ER_1 and the negative components, respectively, are plotted as functions of the intensity of the background noise. The ER_1 becomes almost undetectable at noise levels above approximately -50 db (re 0.01 volt rms into the loud-speaker) while the negative component is still large. At this intensity of noise the clicks are still clearly audible to the experimenter through monitor earphones. At still higher levels of noise (greater than -30 db) the clicks can no longer be detected by the experimenter, and the entire ERC, including the late negative component, disappears. The effect of background noise in selectively reducing the ER_1 has been demonstrated repeatedly in each of four different animals.

The demonstration that the ER_1 can be almost entirely eliminated with little reduction

in the later negative component is strong evidence that the later deflections in the ERC may not be dependent upon the presence of a synchronized ER_1.[2] These facts may be interpreted as follows. The ER_1 reflects activity arriving by one pathway, while the later negative component reflects activity arriving by another. The pathway that gives rise to ER_1 may thus be highly sensitive to background noise under our experimental conditions, while the activity in the other pathway may be much less so. This interpretation, according to which the early and late components of the ERC may represent activity from separate pathways, is consistent with the demonstrated existence of multiple pathways to the cortex.[3-5]

<div align="right">D. C. Teas, N. Y-S. Kiang</div>

References

1. D. C. Teas and N. Y-S. Kiang, Evoked cortical responses as a function of "state" variables, Quarterly Progress Report No. 63, Research Laboratory of Electronics, M.I.T., October 15, 1961, pp. 171-176.

2. M. H. Goldstein, Jr. and N. Y-S. Kiang, Synchrony of neural activity in electric responses evoked by transient acoustic stimuli, J. Acoust. Soc. Am. 30, 107-114 (1958).

3. J. Hanberry and H. Jasper, Independence of diffuse Thalamo-cortical projection system shown by specific nuclear destructions, J. Neurophys. 16, 252-271 (1953).

4. R. Galambos, R. E. Myers, and G. Sheatz, Extra-lemniscal activation of auditory cortex in cats, Amer. J. Physiol. 200, 23-28 (1961).

5. J. Goldberg and W. D. Neff, Frequency discrimination after bilateral section of the brachium of the inferior colliculus, J. Comp. Neur. 116, 265-290 (1961).

C. CONTROL OF EYE MOVEMENTS IN RELATION TO THE VESTIBULAR SYSTEM AND NECK PROPRIOCEPTIVE MECHANISMS IN MAN

A frequently reported symptom of patients who have suffered a loss of vestibular function is a disturbance in visual fixation while they are in motion.[1-4] The disability appears to persist, to some extent at least, permanently.[2] Thus, patients may complain of their vision being "jumbled," or that their eyes feel as though they were "set in Jello," when there is sudden passive movement, as for example when riding in an automobile over a rough road or uneven pavement. It may be impossible for such patients, while walking, to recognize other persons. The great importance of the vestibular apparatus in the stabilization of fixation of gaze has been stressed, on the basis of clinical observations,[1, 3, 4] and an analogy has been made between the aspect of vestibular function and the use of stable platforms in fire control[2]: "The platform which carried telescopes for spotting naval or aerial targets has to be stabilized against roll and change of course and pitch of the battleship ... . In the same way, if the head and the eyes are stabilized against movement of the body, it is possible for the fixation reflex to operate to keep

the target on the fovea." The analogy can equally well be extended to the subsequent use of stabilized platforms in automatic radar-directed fire-control systems,[5] and also to the use of stabilized platforms in inertial guidance systems, particularly those employing automatic star-tracking devices.[6]

In a recent review of the control of eye movements,[2] it was stated: "It is remarkable that there is no coherent view on the relation between reflex mechanisms originating in the neck, labyrinth, and eyes, which act upon the eye muscles." More recently,[7] the importance of neck proprioceptive mechanisms has been re-emphasized.

In an attempt to gain some further understanding of the nature of control of eye movements, both in normal subjects and in patients with absence of labyrinthine function, recordings were made under a variety of conditions from several normal subjects and from a patient who had entirely lost labyrinthine function subsequent to streptomycin toxicity to the vestibular apparatus. Recordings included: (a) the position of one of the eyes, measured electro-oculographically[8, 9] by means of electrodes applied directly above and below the eye (or in the horizontal plane, for horizontal tracking experiments); (b) the position of a spot on an oscilloscope directly in front of the subject's eyes (at a distance of 20 cm); (c) the orientation of the head with respect to the vertical, in an anteroposterior plane, recorded by means of a Grass Instrument Company's accelerometer affixed to the forehead of the subject.

The output of the accelerometer in the earth's gravitational field is proportional to the sine of its angle of inclination with respect to the vertical; for small angles, the output is proportional to the angle. Additional components in the output of the accelerometer which are due to acceleration and deceleration of the head about a horizontal axis, remain small compared with the component that indicates its position in the earth's gravitational field, for frequencies of movement of the head of less than aproximately 3 per second.

Electro-oculographic recording of eye position, in contrast to optical methods[10] (in which a beam of light is reflected off the cornea), permits recordings to be made with the head in motion, or with the eyes closed. In the recordings reported here, bentonite paste electrodes were employed; subsequently, nonpolarizable silver-silver chloride electrodes were employed to avoid the inherent dc drift encountered with bentonite electrodes. Direct-current recordings were made onto paper and onto FM magnetic tape, by means of a Grass Instrument Company's polygraph and a 4-channel push-pull to a single-ended cathode-follower unit, the design of which was provided by Robert Grass of the Grass Instrument Company. The frequency response of the recording system was from dc to 35 cps. All recordings were of 4 minutes duration.

For the study of eye movements in tracking experiments, techniques of analysis and displays basically in the frequency domain have often been used.[11-13] The displays employed with frequency-domain analysis, however, do not permit a direct and ready

comparison of results with those from conventional reaction-time experiments[13] nor with results of studies of cerebral evoked responses.[14]

For the analysis of the present recordings, time-domain analysis in the form of autocorrelation and crosscorrelation was employed. Autocorrelograms provide a summary display of the statistical characteristics of the signal in each instance, and crosscorrelograms provide a direct display of time relationships between signals, averaged over the 4-minute recordings in each case. For analysis, the original magnetic-tape recordings were speeded up 50 or 100 times. Autocorrelograms were computed at
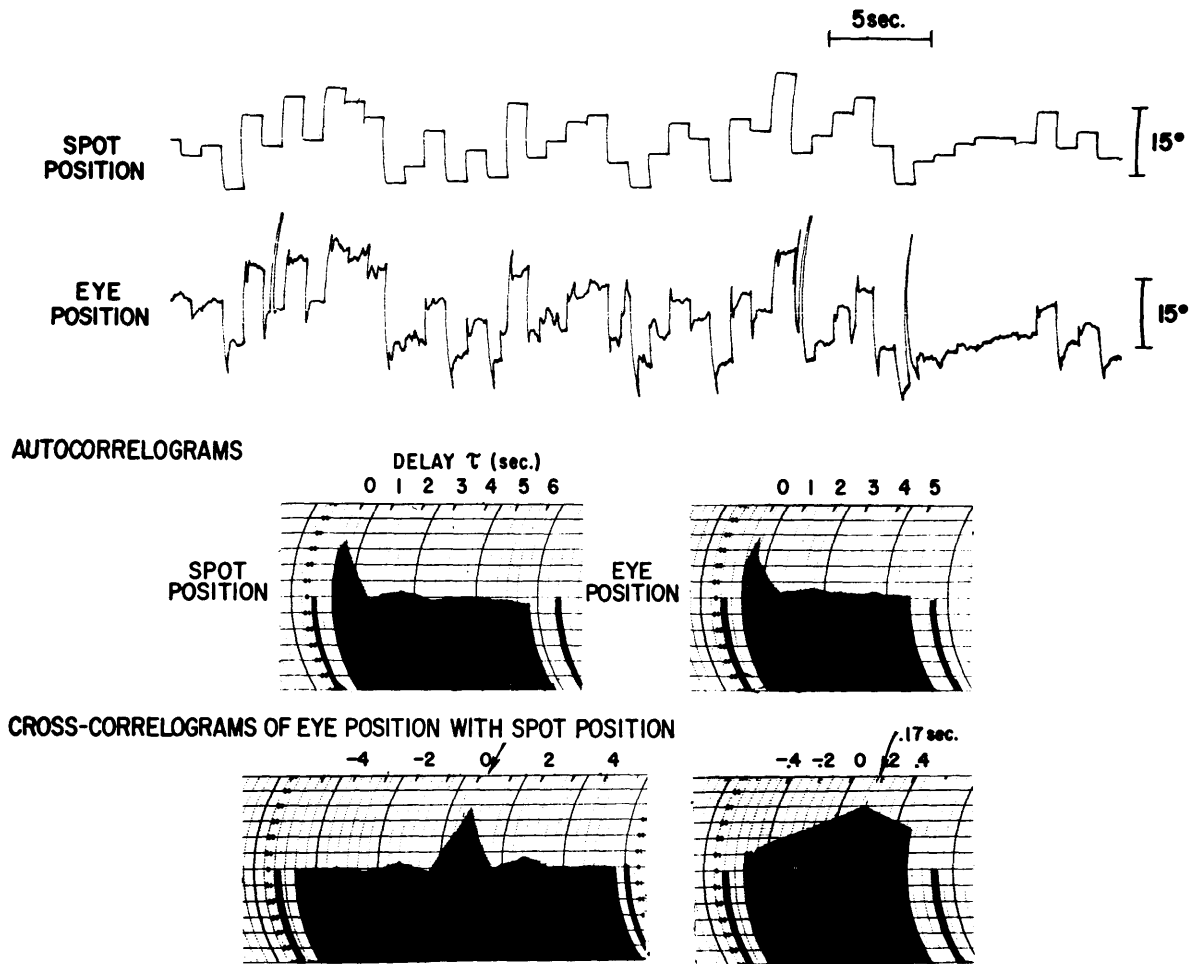

Fig. XVIII-6. Vertical tracking of a randomly repositioned spot, head fixed. Interval between successive repositionings of spot, 1 sec. Eye-scope distance, 20 cm. Duration of recording analyzed, 4 minutes. The calibrations for position of spot and for position of eye is approximately the same for Figs. XVIII-7 through XVIII-18. Delay scale is in seconds. The arrow indicates the peak in the crosscorrelogram, and refers to average oculomotor reaction time. (Subject: J.B.)
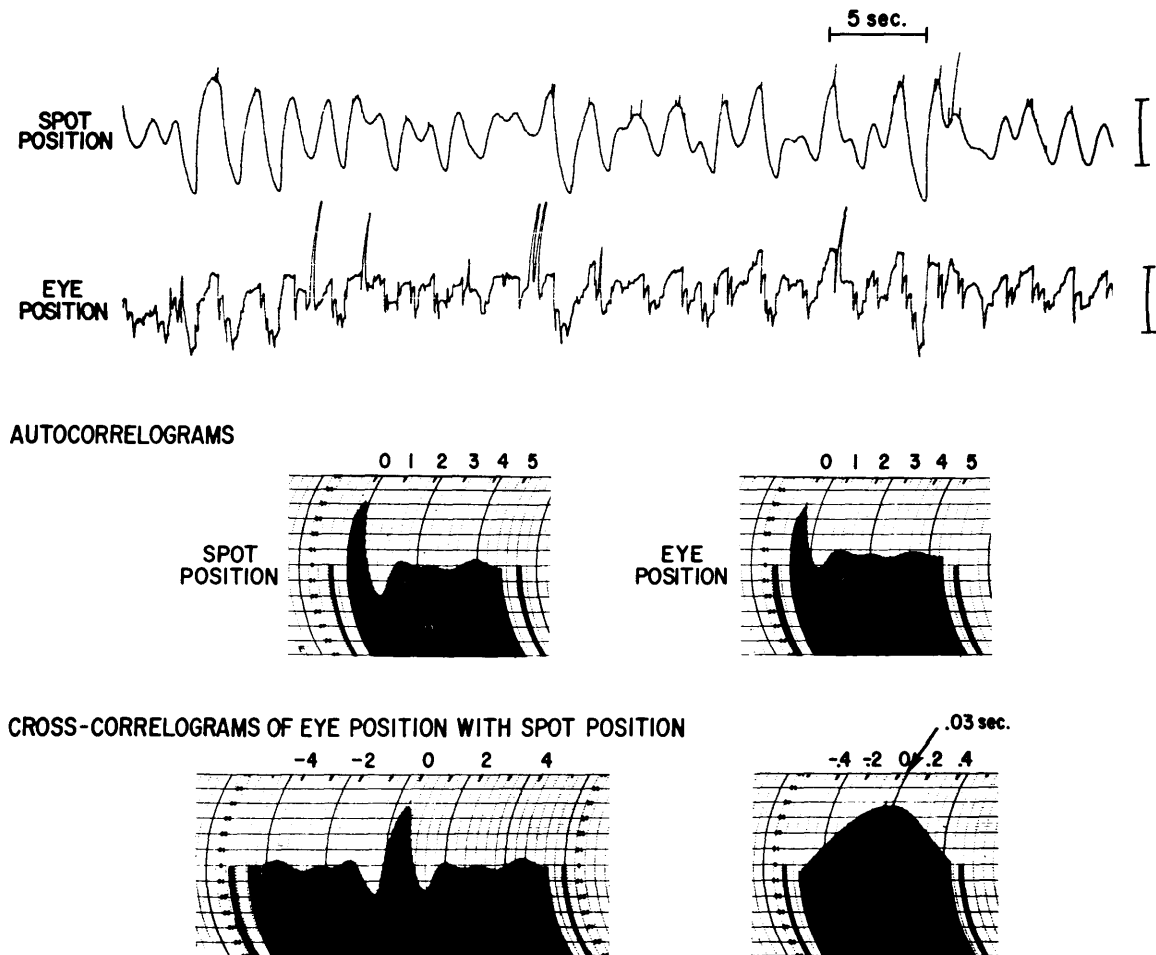
Fig. XVIII-7.   Vertical tracking of a randomly moving spot; head fixed.   Amplitude
and calibration for spot and eye positions approximately the same as
in Fig. XVIII-6.   (Subject: J.B.)

50-msec delay ($\Delta\tau$) intervals; crosscorrelograms at 50- and 10-msec $\Delta\tau$ intervals.

Results of recordings from a normal subject are shown in Figs. XVIII-6 through
XVIII-11.   As a preliminary part of the experiment, an attempt was made to determine
oculomotor reaction time.   For this purpose, recordings were made while the subject
was attempting to fixate on a spot on the oscilloscope which was periodically repositioned
to a new vertical location that was independent of the previous location.   Such a signal,
as the input for the vertical deflection plates of the oscilloscope, was obtained by means
of a noise generator and one of the sample-and-hold circuits available in the Analog
Computer for Neurophysiology[15, 16] located in the Neurophysiology Laboratory of the
Massachusetts General Hospital.

Results from this preliminary experiment, together with a portion of the corre-
sponding ink traces, are shown in Fig. XVIII-6.   The fact that the autocorrelogram of

the input signal to the vertical axis of the oscilloscope falls to the base line at a delay of 1 sec, and thereafter remains essentially at the base-line level, indicates the unpredictability of successive positions of the spot on the oscilloscope. The autocorrelogram for the position of the eye shows an initially rapidly declining component superimposed on the more steadily declining one that was evident for the spot-position signal; this initially rapidly decaying component is a reflection of the overshoot of eye position that frequently appears immediately upon redirection of the gaze and before the correct fixation point is obtained. The presence of eye-blinks in the recording also contributes to this initial component. An average reaction time before initiation of ocular movements, which follows each change of spot position, is seen from the crosscorrelograms to be approximately 170 msec.

The subject, with head fixed, was then required to track a continuously moving spot
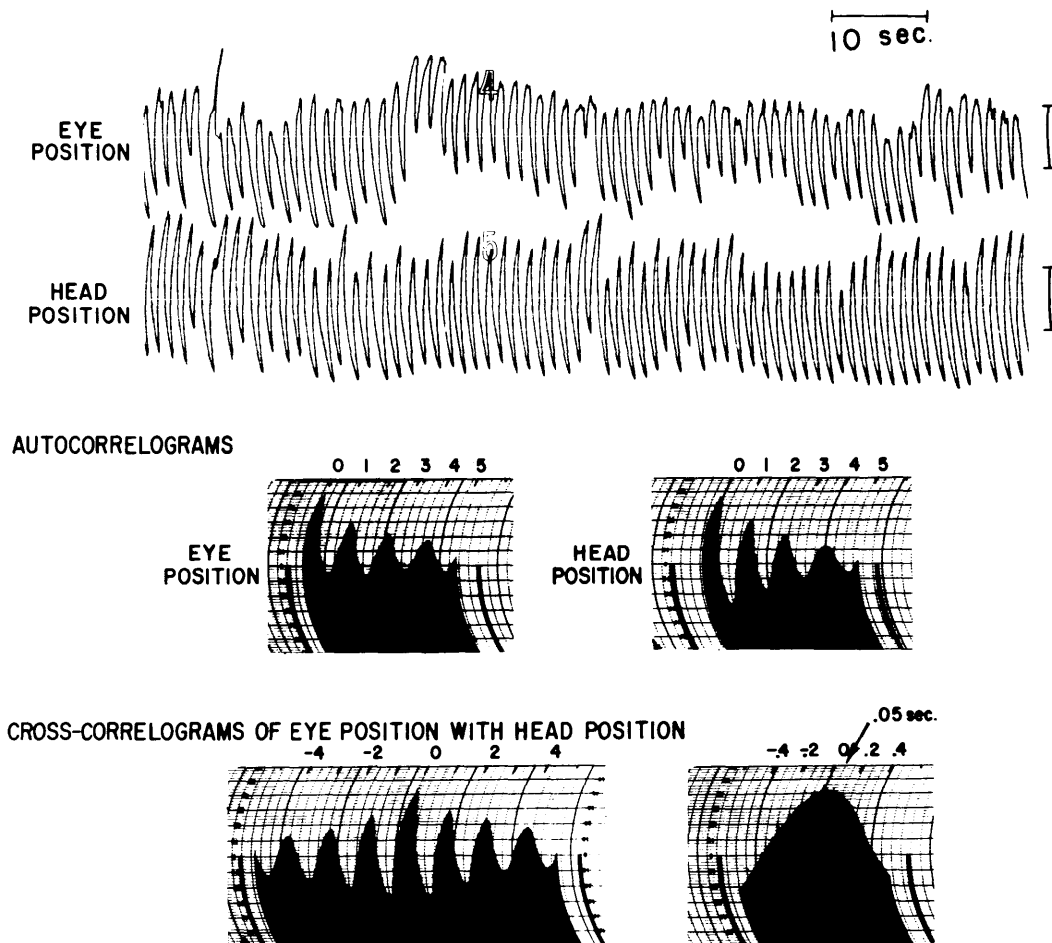

Fig. XVIII-8. Tracking of fixed spot; passive vertical rotation
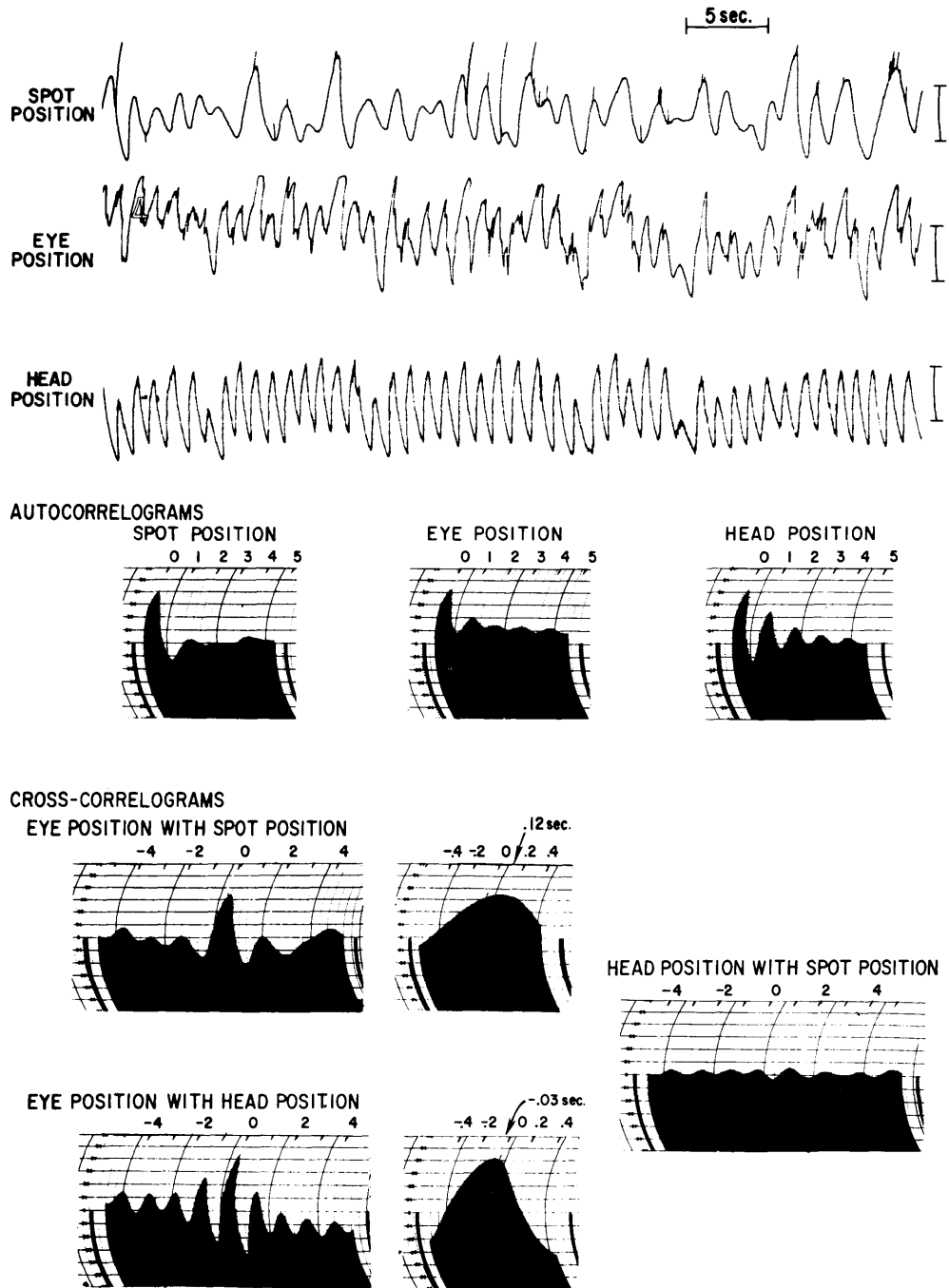of the head. (Subject: J.B.)

Fig. XVIII-9. Vertical tracking of a randomly moving spot; passive movement of head. (Subject: J.B.)
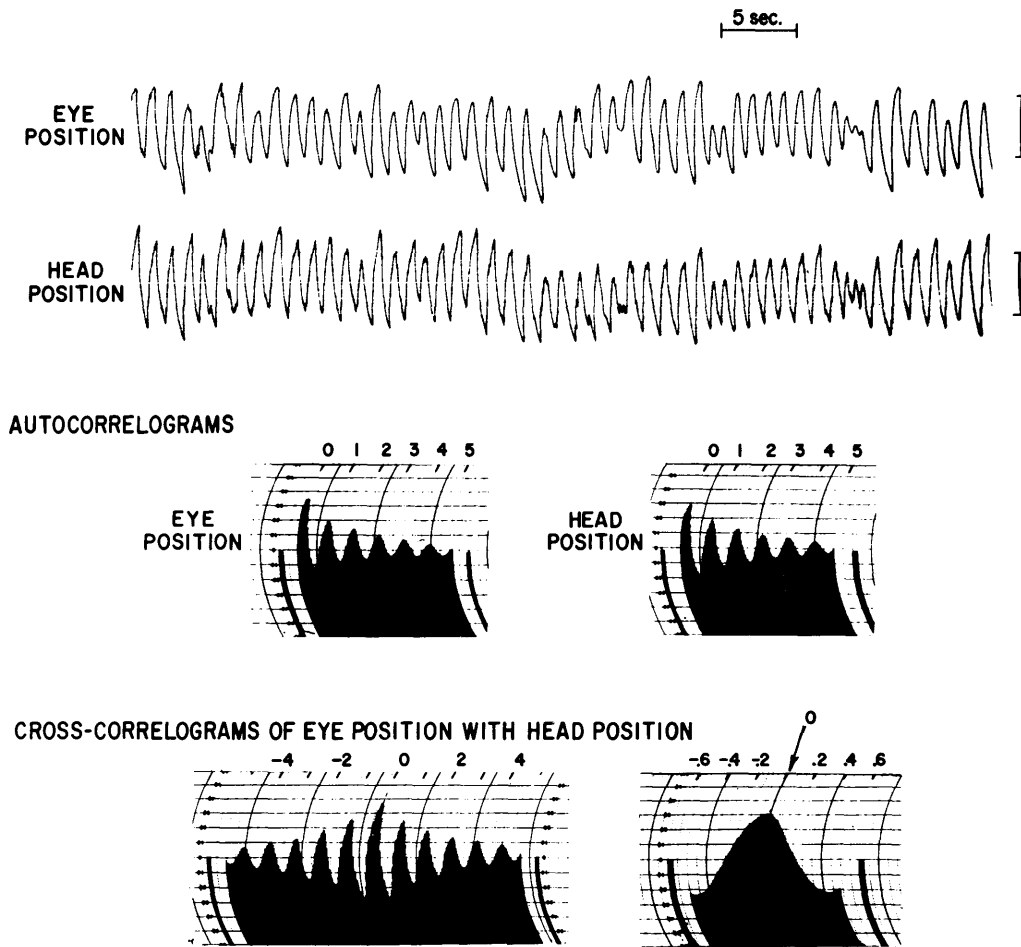
Fig. XVIII-10. Tracking of fixed spot; active vertical rotation of head. (Subject: J.B.)

on the oscilloscope; for this purpose the vertical-axis input was a random signal that had been prerecorded at a higher speed onto the same tape. Autocorrelograms for the noise signal and eye position, and the crosscorrelogram for these two, are shown in Fig. XVIII-7. It is apparent that the general shape of the two autocorrelograms is much the same, and the fact that the peak of the crosscorrelogram occurs very close to zero delay (0.03 sec) indicates an average tracking with very little time delay.

In Fig. XVIII-8, results are shown from a recording during which the spot on the oscilloscope was kept fixed, and the subject fixated on the spot while the experimenter rotated the subject's head by hand about an axis through the neck and parallel to the shoulders (i.e., flexion and extension of the neck). In the ink trace (for which one-half of the usual paper speed was used), the position of the eye is indicated in the upper trace, and the angular position of the head, as monitored by the accelerometer, is shown in the lower trace. In this recording, the distance between the eye and the oscilloscope

screen was approximately 25 cm. The similarity between the autocorrelogram for head position and that for eye position is evident. The crosscorrelograms for these two indicate that the eye position lagged the head position by an average of approximately 50 msec.

In Fig. XVIII-9 are shown results obtained from a recording for which the subject was visually tracking the randomly moving spot on the oscilloscope at the same time that his head was being passively moved. Autocorrelograms are shown for the position of the spot on the oscilloscope screen, the position of the eyes, and the position of the head. It is apparent that the average frequency of movement of the head was somewhat greater than that of the randomly moving spot. Crosscorrelograms are shown for the eye position with spot position, eye position with head position, and head position with spot position, respectively. When the position of the eyes is crosscorrelated with the position of the spot, it is apparent that there is a lag of approximately 120 msec of eye
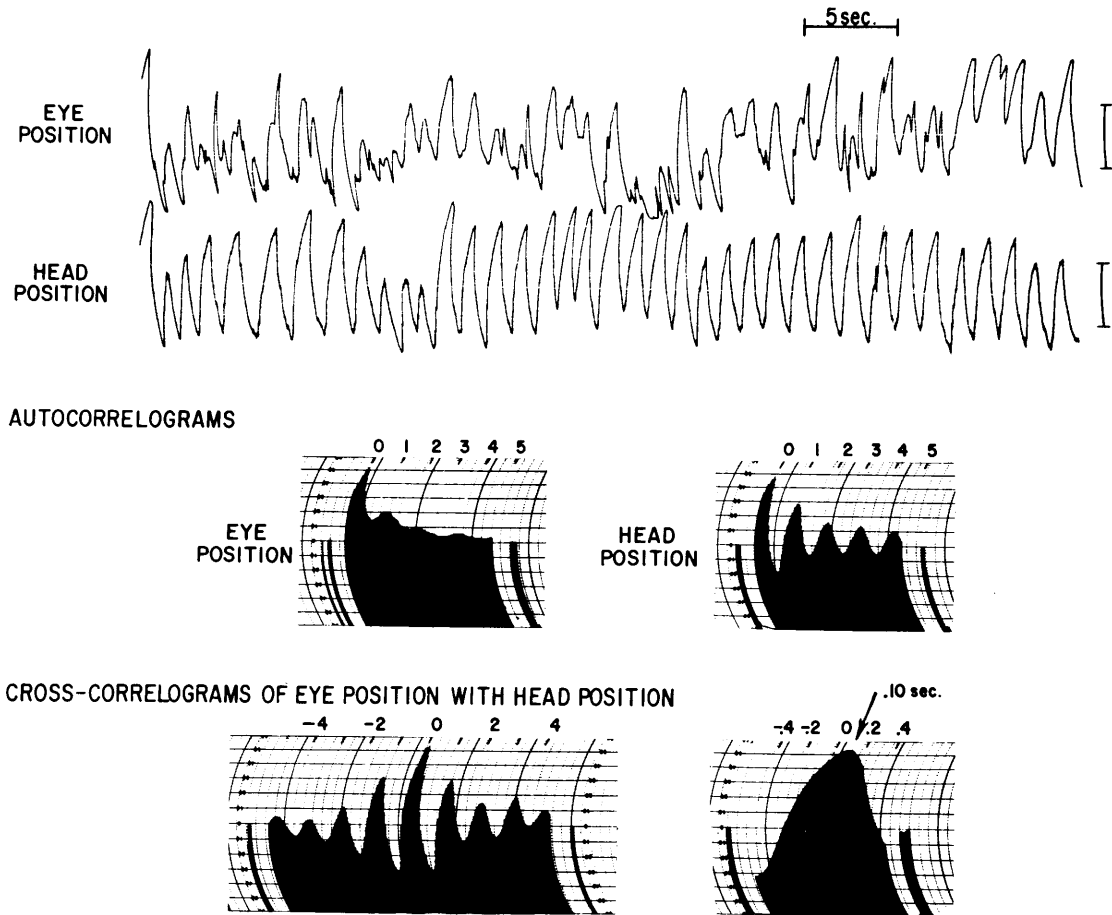

Fig. XVIII-11. Relation between eye position and head position for passive vertical rotation of head; eyes closed. (Subject: J.B.)
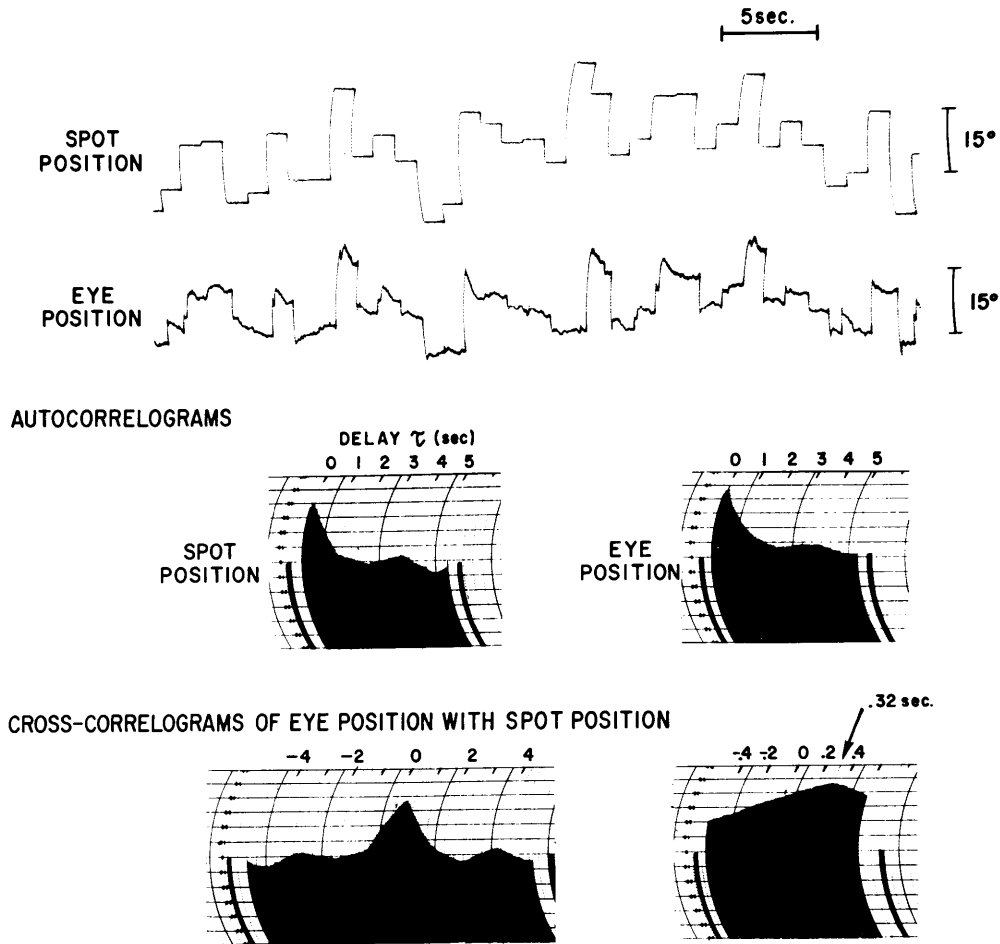
5sec.

SPOT
POSITION

15°

EYE
POSITION

15°

AUTOCORRELOGRAMS

DELAY 𝒯 (sec)

0 1 2 3 4 5

0 1 2 3 4 5

SPOT
POSITION

EYE
POSITION

CROSS-CORRELOGRAMS OF EYE POSITION WITH SPOT POSITION

.32 sec.

-4 -2 0 2 4

-4 -2 0 .2 .4

Fig. XVIII-12.   Vertical tracking of a spot randomly repositioned every 1.2 sec;
head fixed. (Subject: W. T.)

position with respect to spot position. On the other hand, crosscorrelation of the eye
position with the head position indicates that the position of the eyes was slightly antic-
ipatory to that of the head, by approximately 30 msec. In this recording the movement
of the head was independent of that of the spot, and therefore the crosscorrelogram of
these two is essentially flat, except for minor irregularities arising from sampling
artefact which would decrease progressively as the length of the recording is increased.

Results from a recording for which the spot on the oscilloscope was maintained in
a fixed position and the subject was actively moving his own head while directing his
gaze at the spot are shown in Fig. XVIII-10. The average frequency of movement of
head is approximately 1.1 per sec, and it is of interest that there appears to be no time
lag between eye position and head position, in contrast to the lag of approxi-
mately 50 msec which appeared when the subject's head was being passively
moved (Fig. XVIII-8).

From the ink recordings of eye movements in Figs. XVIII-7, XVIII-8, XVIII-9, and XVIII-10, it is apparent that the traces of eye movements in Figs. XVIII-8 and XVIII-10 (spot fixed, head moving) are considerably smoother than that in Fig. XVIII-7 (head fixed, spot moving). The tracing of eye movement in Fig. XVIII-9 (head and spot moving) is intermediate in smoothness between these two extremes.

In Fig. XVIII-11, results are shown of a recording for which the subject's head was being moved while his eyes were kept closed. The tracing of eye position once again assumes a somewhat irregular character (compare its autocorrelogram with that for eye position in Fig. XVIII-10). In general, it remains correlated with the position of the head, but lags the head by approximately 100 msec, an appreciably greater time lag than that observed with eyes open (Figs. XVIII-7 through XVIII-10).

Results of recordings from a patient who had suffered loss of vestibular function following streptomycin toxicity to the vestibular apparatus (hearing remained intact)
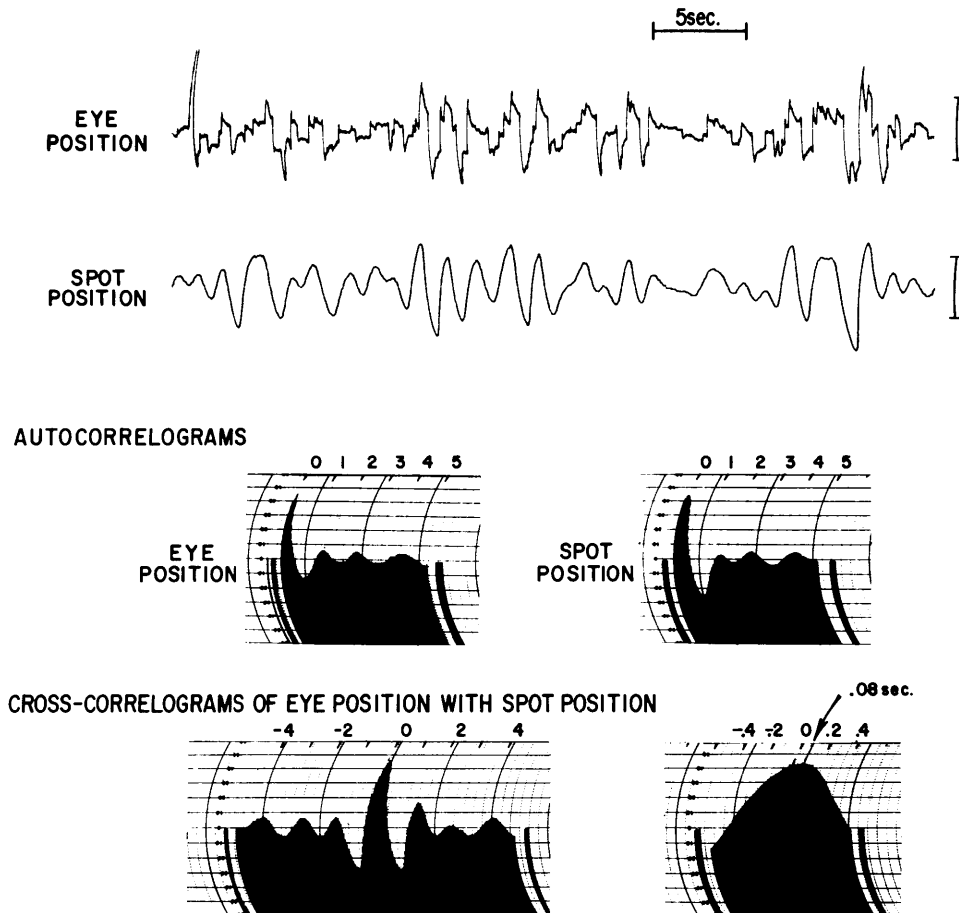

Fig. XVIII-13. Vertical tracking of a randomly moving spot; head fixed. (Subject: W.T.)

are shown in Figs. XVIII-12 through XVIII-18. In Fig. XVIII-12 are shown results of vertical visual tracking of an unpredictable signal of the same type as that in Fig. XVIII-6, except that the time interval between random repositioning was 1.2 sec instead of 1.0 sec. It is apparent that there is a greater difference between these two autocorrelograms than for the pair of autocorrelograms in Fig. XVIII-6, a difference suggesting poorer tracking by subject W.T. which is substantiated by comparison of the inked traces in Figs. XVIII-6 with those of Fig. XVIII-12. The average latency of oculomotor response in Fig. XVIII-12 is seen from the crosscorrelograms to be approximately 320 msec, appreciably longer than the one of 170 msec which is apparent in Fig. XVIII-6.

Results of tracking a continuously moving spot (motion of the same type as was used for Fig. XVIII-7) on the oscilloscope screen, the head remaining fixed, are shown in Fig. XVIII-13. The crosscorrelograms for eye position with spot position indicate that
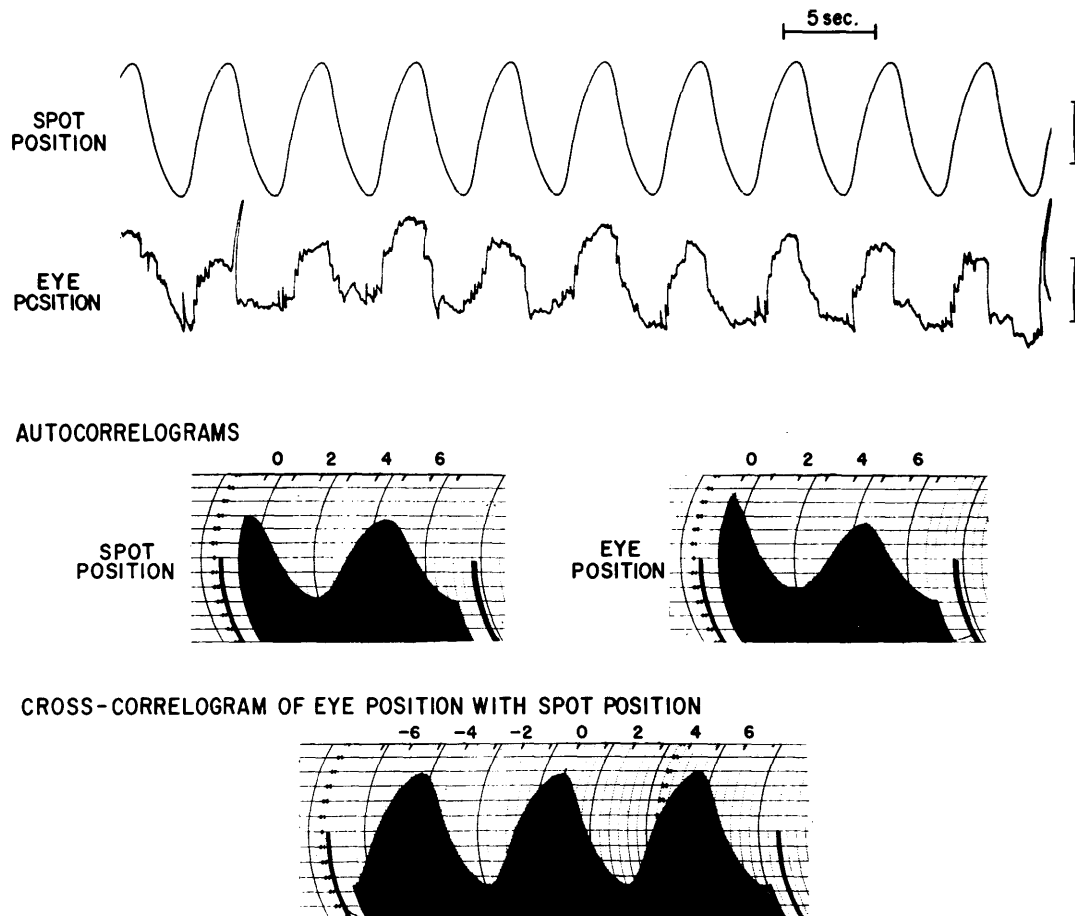

Fig. XVIII-14. Vertical tracking of a sinusoidally moving spot; head fixed. (Subject: W.T.)

the eye position lags the spot position by approximately 80 msec.

In Fig. XVIII-14 are shown corresponding results of visual tracking of a vertical sinusoidally moving spot, the frequency of the motion being 0.2 per second. The cross-correlogram shows that the position of the eye movement is essentially in phase with that of the spot, possibly anticipating the latter very slightly.

In Fig. XVIII-15 are shown results of a recording made while the subject's head was being moved at the same time that he was fixating on the spot on the oscilloscope, itself immobile, the oscilloscope being approximately 25 cm from the subject's eyes. The eye position is seen to be a very faithful replica of the head position; the tracking in this recording is obviously much better than that in Fig. XVIII-14, even though the signal was of a much slower and simpler nature in the latter. From the crosscorrelograms it is evident that the position of the eye lagged that of the vertical position of the head by approximately 70 msec.
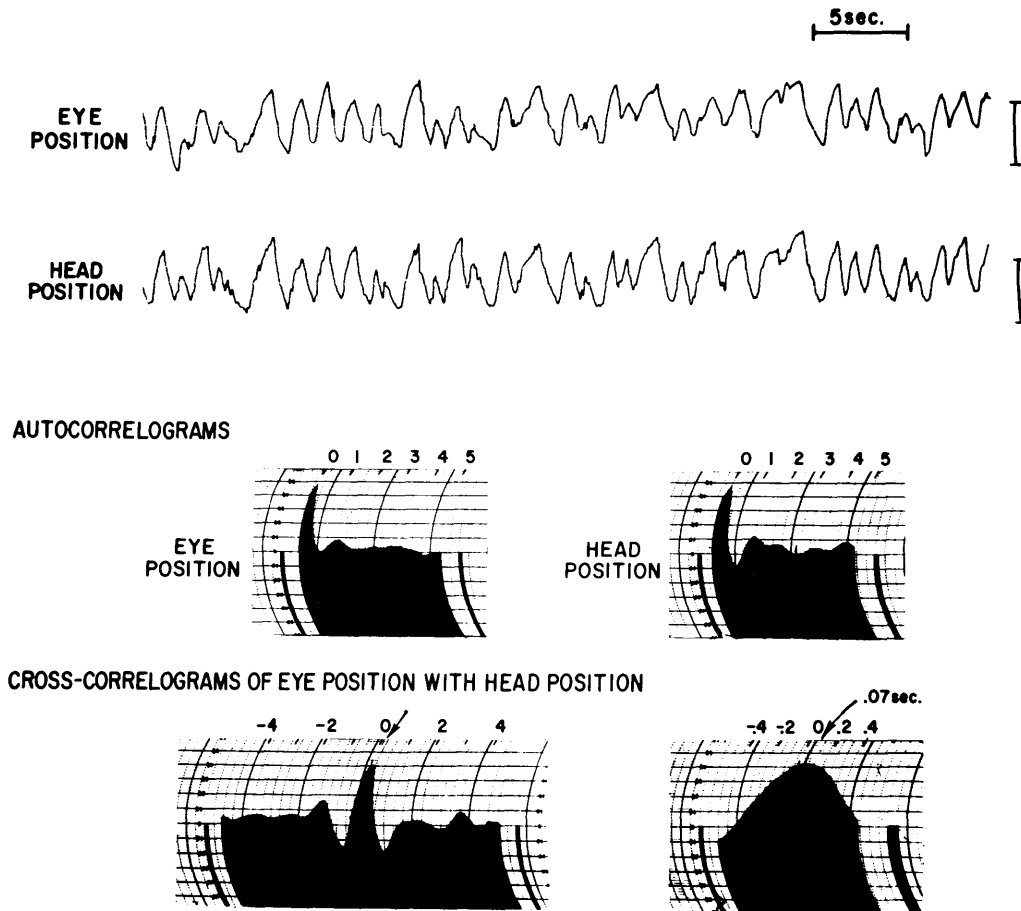

Fig. XVIII-15. Tracking of a fixed spot; passive vertical rotation of head. (Subject: W.T.)
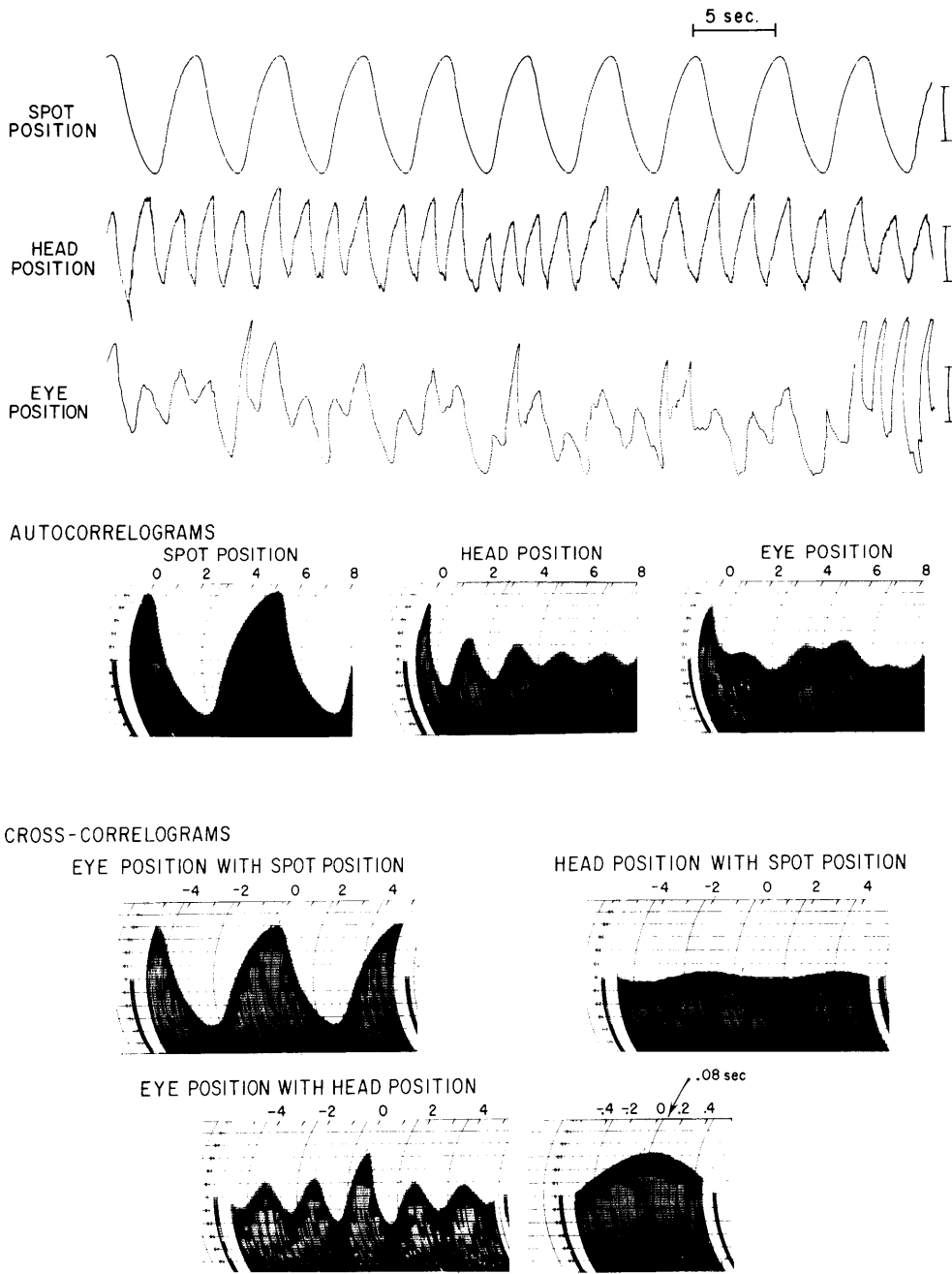
216

5 sec.

SPOT
POSITION

HEAD
POSITION

EYE
POSITION

AUTOCORRELOGRAMS

SPOT POSITION
0   2   4   6   8

HEAD POSITION
0   2   4   6   8

EYE POSITION
0   2   4   6   8

CROSS-CORRELOGRAMS

EYE POSITION WITH SPOT POSITION
-4   -2   0   2   4

HEAD POSITION WITH SPOT POSITION
-4   -2   0   2   4

EYE POSITION WITH HEAD POSITION
-4   -2   0   2   4

.08 sec
-4 -2 0 .2 .4

Fig. XVIII-16.   Vertical tracking of a sinusoidally moving spot; passive
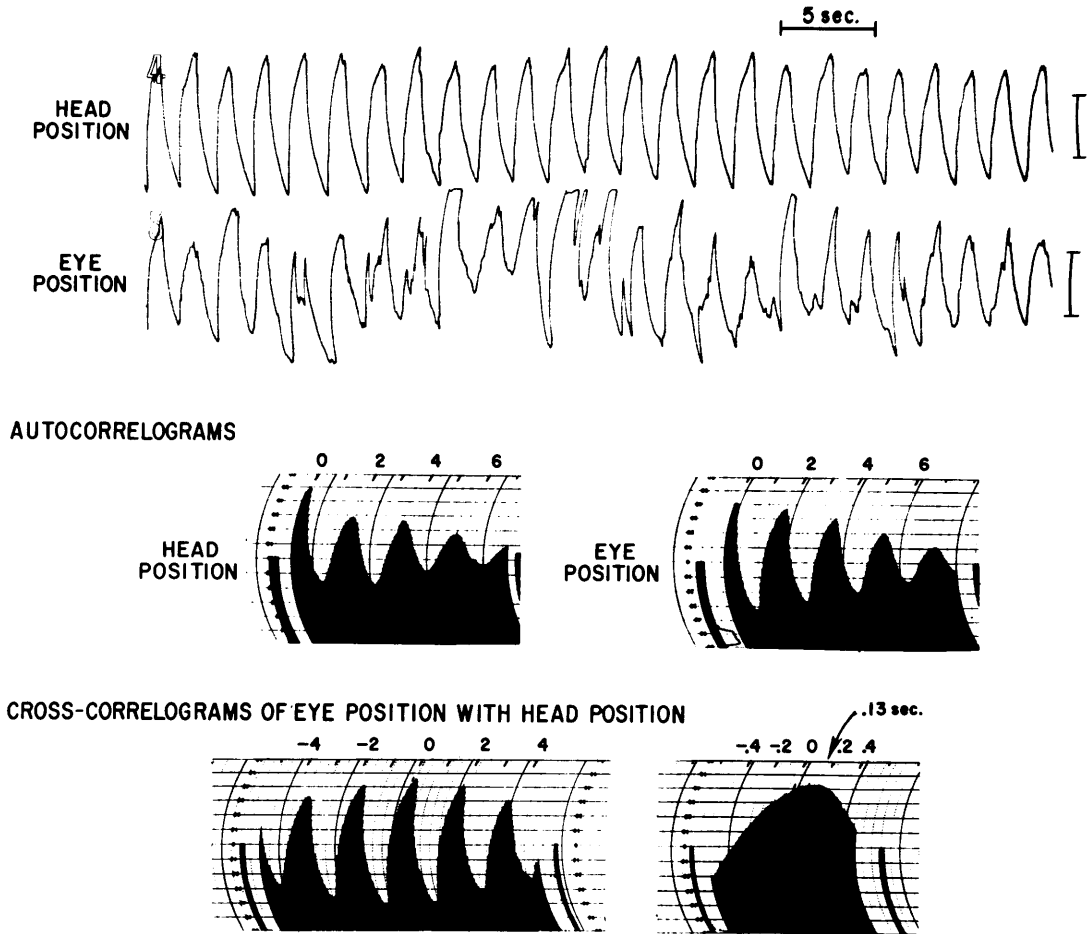movement of head.   (Subject: W.T.)

217

Fig. XVIII-17. Tracking of a fixed spot; active vertical rotation of head. (Subject: W. T.)

In Fig. XVIII-16 are shown results of a recording for which the subject's head was being moved passively at the same time that he was attempting to track visually the sinusoidally moving spot on the oscilloscope. The average frequency of movement of the head was approximately 0.5 per second. The autocorrelogram of eye movement represents the sum of the autocorrelograms of the spot position and of head position. In the crosscorrelogram of eye position with spot position, it is apparent that the eye position is essentially in phase with the spot position, whereas from the crosscorrelo-gram of head position with eye position, the eye position lags the head position by approximately 80 msec. Spot position and head position were, of course, uncorrelated, and this fact is reflected by an essentially flat crosscorrelogram of these two, as shown in the figure.

In Fig. XVIII-17 are shown results of a recording for which the subject moved his own head while fixating on an immobile spot. The average frequency of head movement

is 0.45 per second. The crosscorrelograms reveal that eye position lagged head position by approximately 130 msec. It is puzzling that the tracking in this figure is poorer, and the latency greater, than for passive movement of the head which is shown in Fig. XVIII-15.

In Fig. XVIII-18 are shown results of horizontal tracking of a sinusoidally moving spot on the oscilloscope, the head of the subject remaining fixed, for comparison with the vertical tracking shown in Fig. XVIII-12. It is interesting, from the correlogram of this figure, that the position of the eye tended to lead that of the spot by approximately 250 msec, a fact that indicates an anticipatory movement of the eyes in this horizontal tracking problem. The quality of the horizontal tracking is obviously superior to that of the vertical tracking shown in Fig. XVIII-12.

From a comparison of the results of analyses of the recordings from the patient with absent vestibular function with those for the normal subject, it is apparent that
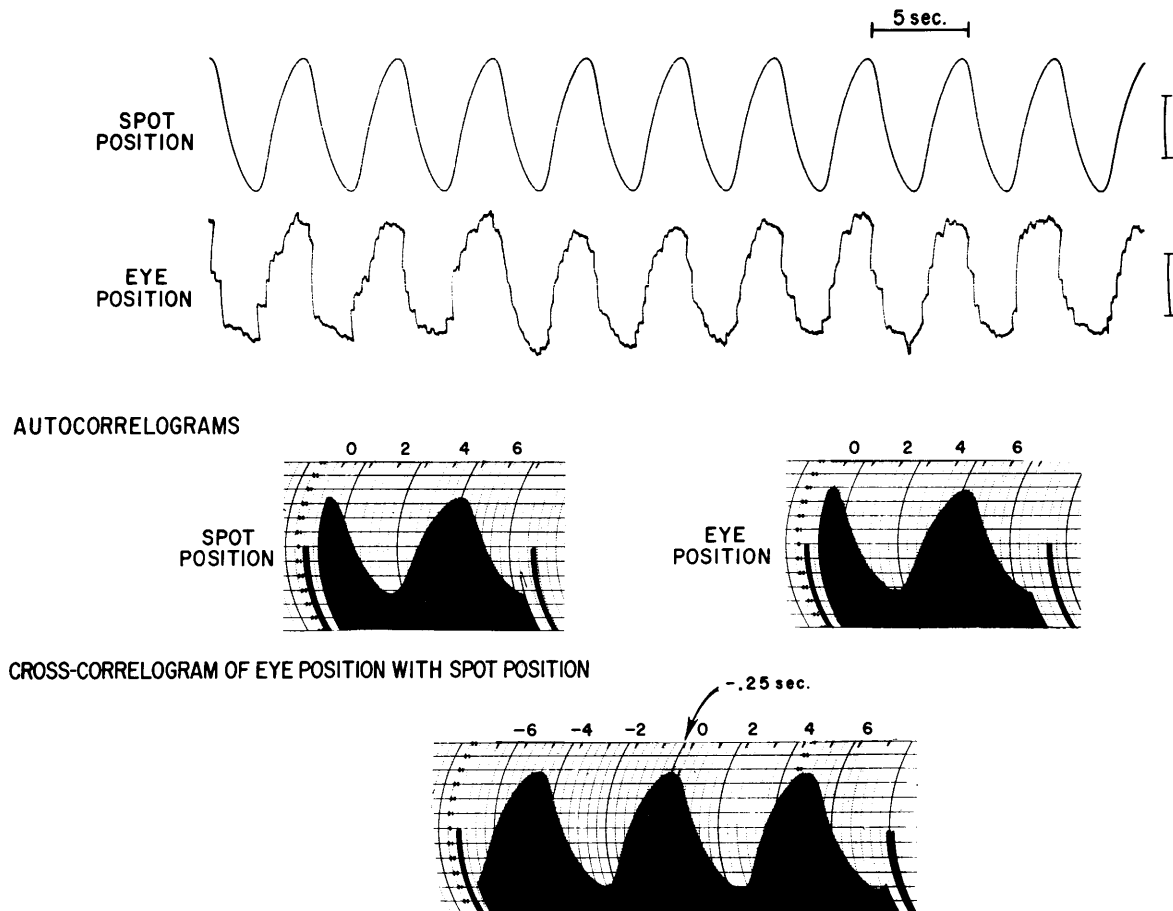
Fig. XVIII-18. Horizontal tracking of sinusoidally moving spot; head fixed. (Subject: W. T.)

there is still remarkably good compensatory motion of eyes accompanying either active or passive motion of head; this result suggests that the vestibular apparatus does not play an essential role in the control of compensatory eye movements when the head is moved, if the body itself remains stationary, at least for relatively low frequencies of movements of the head. Because of the nature of the experimental arrangement, similar quantitative studies could not be carried out to determine results for sudden head movements, either active or passive.

The fact that compensatory eye movements, in response to movements of the head, were well carried out by the patient was substantiated by qualitative experiments in which the patient was asked to read a newspaper at the same time that his head was being passively moved through excursions similar to or greater than those shown in Figs. XVIII-15 and XVIII-16. During passive movements of the head, of this type, the patient had no difficulty in reading, but there was difficulty if sudden movements of the head were induced, either passively or actively.

It would be of interest to carry out these experiments while the entire body were moved up and down, for example on an electrically operated barber's or dentist's chair, or if the body were rotated about a horizontal axis passing through the eyes or neck. Such an arrangement would permit the neck to remain stationary with respect to the body, thus eliminating the role of neck proprioceptive mechanisms from oculomotor tracking. The necessary experimental arrangement would, of course, be considerably more complicated than the one used in the present experiments.

In conclusion, the present results strongly suggest that proprioceptive information derived from the muscles and joints of the neck have a considerable importance in visual tracking carried out while the head is moved with respect to the body, if the latter remains stationary.

J. S. Barlow

References

1. F. R. Ford and F. B. Walsh, Clinical observations upon the importance of the vestibular reflexes in ocular movements, Bull. Johns Hopkins Hosp. 58, 80-88 (1936).

2. D. Whitteridge, Central control of eye movements, Handbook of Physiology, edited by J. Field (American Physiological Society, Washington, D.C., 1960), Section I (Neurophysiology), Vol. 2, Chapter 42, pp. 1089-1109.

3. D. G. Cogan, Some objective and subjective observations on the vestibulo-ocular system, Am. J. Ophthalmol., Vol. 45, No. 4, Part II, pp. 74-78, 1958.

4. J. Crawford, Living without a balancing mechanism, New England Journal of Medicine 246, 458-460 (1952).

5. W. Wrigley and J. Hovorka, Encyclopedia of Fire Control, Vol. 1, Fire Control Principles, Instrumentation Laboratory, M.I.T., 1957.

6. R. B. Horsfall, Stellar inertially navigation, Trans. IRE Vol. ANE-5, pp. 106-114, 1958.

7. L. A. Cohen, Role of eye and neck proprioceptive mechanisms in body orientation and motor coordination, J. Neurophysiol. 24, 1-11 (1961).

8. O. H. Mowrer, T. C. Ruch, and N. E. Miller, The corneo-retinal potential difference as the basis of the galvanometric method of recording eye movements, Am. J. Physiol. 114, 423-428 (1936).

9. C. Kris, Vision: Electro-oculography, Medical Physics, Vol. 3, pp. 692-700, 1960.

10. L. Stark and A. Sandberg, A simple instrument for measuring eye movements, Quarterly Progress Report No. 62, Research Laboratory of Electronics, M.I.T., July 15, 1961, pp. 268-270.

11. D. Trincker, J. Sieber, and J. Bartual, Schwingunganalyse der vestibular, optokinetisch und durch elektrische Reizung ausgelösten Augenbewegungen beim Menschen, Kybernetik 1, 21-28 (1961).

12. D. H. Fender and P. W. Nye, An investigation of the mechanism of eye movement control, Kybernetik 1, 81-88 (1961).

13. L. Stark, G. Vossius, and L. R. Young, Predictive control of eye movements, Quarterly Progress Report No. 62, Research Laboratory of Electronics, M.I.T., July 15, 1961, pp. 271-282.

14. J. S. Barlow, Rhythmic activity induced by photic stimulation in relation to intrinsic alpha activity of the brain in man, EEG Clin. Neurophysiol. 12, 317-326 (1960).

15. J. S. Barlow, A versatile analog computer for neurophysiological research, Quarterly Progress Report No. 61, Research Laboratory of Electronics, M.I.T., April 15, 1961, pp. 184-186.

16. J. S. Barlow, A versatile analog computer for neurophysiological research, Digest of the 1961 International Conference of Medical Electronics, New York, July 21-28, 1961, p. 27.

D. SIMULATION OF NORMAL AND ABNORMAL ELECTROENCEPHALOGRAMS

In Quarterly Progress Report No. 54 (pp. 173-180), it was pointed out that in crosscorrelograms for EEG from homologous locations on the two hemispheres of patients with unilateral cerebral disease and a concomitant unilateral slow-wave abnormality, there may be an asymmetry about the point $\tau = 0$, whereas crosscorrelograms for normal subjects appeared to be invariably symmetrical in this respect. In Quarterly Progress Report No. 61 (pp. 166-172), crosscorrelograms for pharmacologically induced unilateral EEG abnormality were shown which did not show such an asymmetry. Illustrative examples are reproduced in Figs. XVIII-19, XVIII-20, and XVIII-21. In an attempt to gain further understanding of the nature and significance of abnormal, as well as normal, EEG activity, mock-up experiments were carried out, and the results of
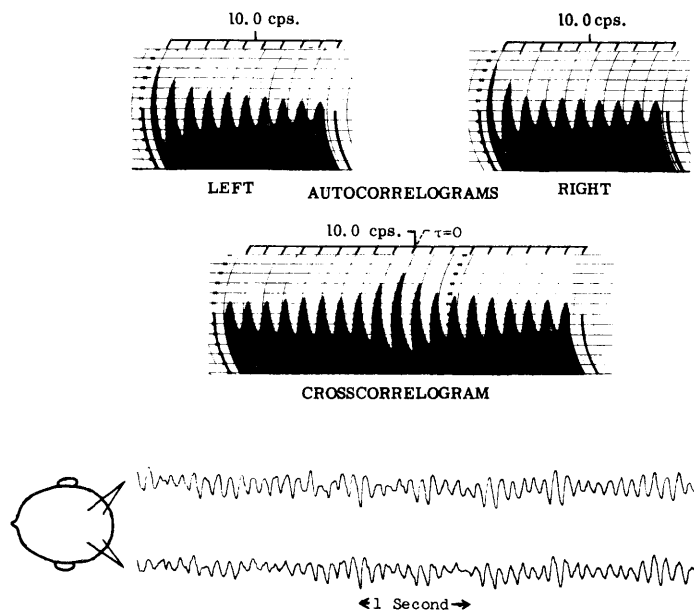
Fig. XVIII-19. Autocorrelograms and crosscorrelograms for a 1-minute
simultaneous left parieto-occipital recording from a normal
human subject.

some preliminary attempts to simulate normal and abnormal EEG and symmetrical and
asymmetrical crosscorrelograms are reported here.

In the choice of the signals for the mock-up experiments, three factors were con-
sidered. First, from inspection of Fig. XVIII-20, it is apparent that the crosscorrelo-
gram obtained when the EEG from the right side is <u>advanced</u> in time (in the computational
procedure) with respect to that on the left is different from that obtained when the EEG
from the right side is <u>delayed</u> in time with respect to that on the left (left and right
halves, respectively, of the crosscorrelogram). This difference indicates that the EEG
for the two sides were not symmetrical about any arbitrary point in time, a comparison
that is shown schematically in Fig. XVIII-22. Second, it was apparent that the basic
signals to be used in the simulation experiments should be of a random, rather than a
periodic, nature, since the autocorrelograms for resting EEG, both for normal subjects
and for patients with brain disease, are clearly not of a truly periodic nature. Third, it
appears likely that those influences that tend to synchronize EEG activity recorded at
homologous locations on the scalp[1] act, at least in part, by means of propagated nerve
impulses, rather than by means of graded-response phenomena.[2]

With these considerations in mind, we employed trains of randomly recurring pulses
from which "slow-wave" activity of normal and abnormal types were then derived. In
Fig. XVIII-23 the transformations that were employed to obtain the derived slow waves
are illustrated. For this purpose, a tuned circuit and a lowpass filter were employed;

the unit impulse responses of these are indicated in the figure. The randomly recurring pulses shown in the upper right of Fig. XVIII-23 were obtained by means of Tektronix Corporation Type 161 and Type 162 pulse and waveform generator, triggered by means of a source of wideband random noise. The outputs of the tuned circuit and of the low-pass filter for an input of randomly recurring pulses are shown in the second and third traces on the right in Fig. XVIII-23. Some similarity between the output of the tuned circuit and that of the EEG reproduced in Fig. XVIII-19 is evident; likewise, some similarity is evident between the output of the lowpass filter and the slow-wave activity that is apparent in Fig. XVIII-20 in the EEG recorded from the right side.

Since the EEG from homologously located electrodes, even in normal subjects, is not absolutely the same (Fig. XVIII-19), the arrangement depicted in Fig. XVIII-24 was employed for the purpose of making recordings for correlation analysis. With respect

LEFT   AUTOCORRELOGRAMS   RIGHT
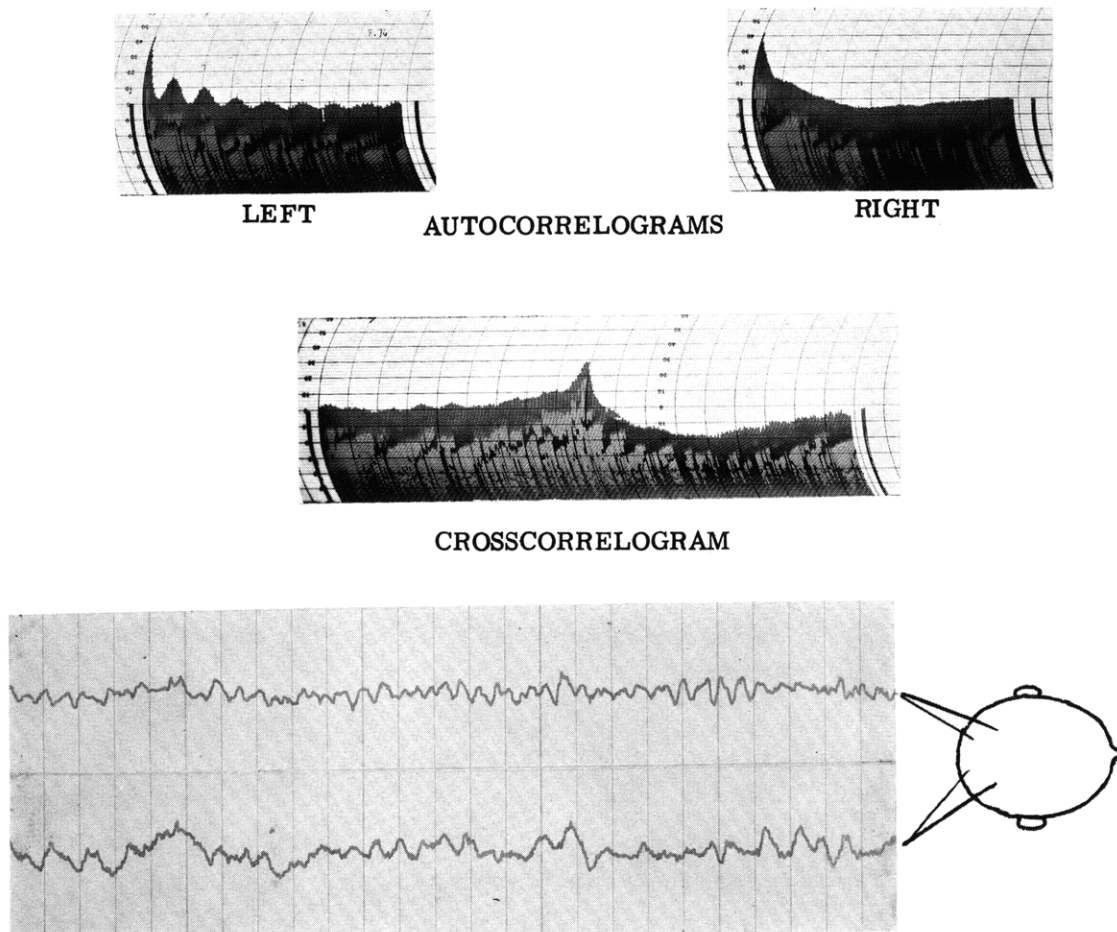
CROSSCORRELOGRAM

Fig. XVIII-20. Autocorrelograms and crosscorrelograms for 1-minute recording from patient with a tumor of the right cerebral hemisphere.
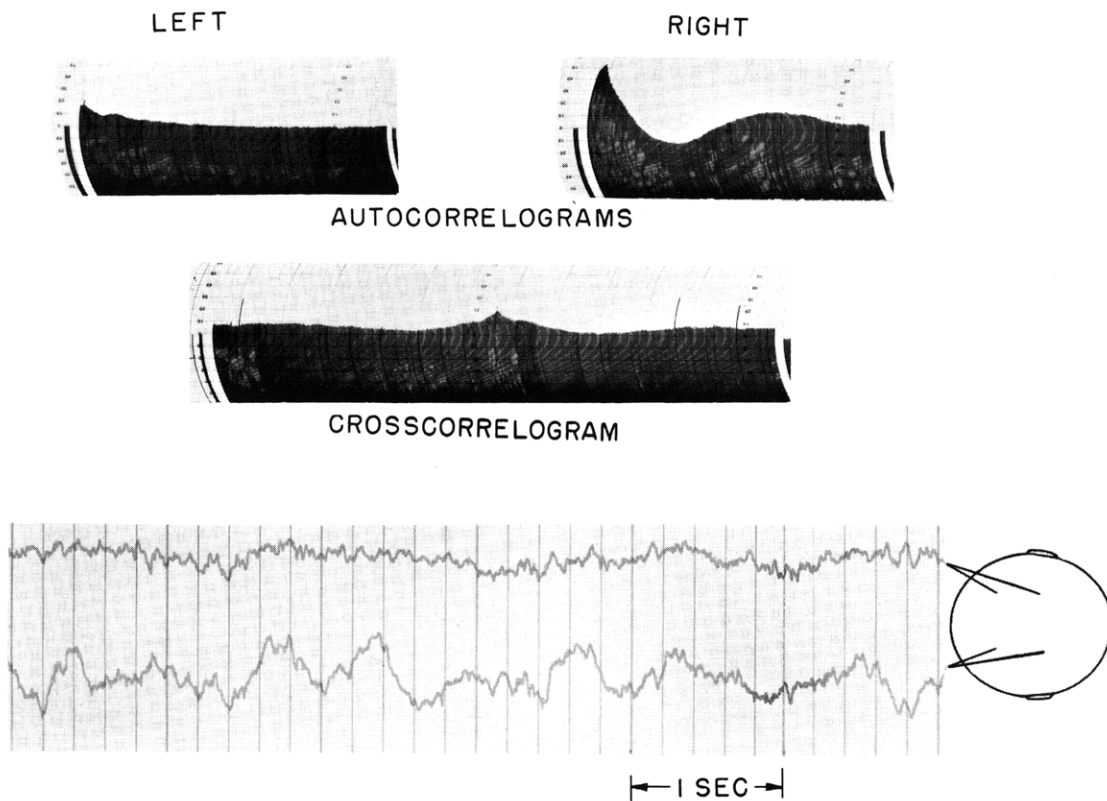
Fig. XVIII-21. Correlograms following right intracarotid injection of 200 mg of sodium amytal; analysis of 1-minute recording.

to an analogy with the electrical activity of the brain, it could be supposed that random pulse generator No. 2 in Fig. XVIII-24 is an analog of a source of neuronal impulses arriving at the cortex bilaterally from deep structures (e.g., ascending reticular formation propagated through the nonspecific thalamic system), whereas the output of random pulse generators No. 1 and No. 3 could be imagined to have their analogs in locally generated electrical activity at the cortex on the left and right sides, respectively, or in activity propagated from paired subcortical nuclei.

Simulated normal EEG and correlograms are shown in Fig. XVIII-25; the symmetry of the crosscorrelogram about the point $\tau = 0$ is evident. A simulated unilaterally abnormal EEG, with corresponding correlograms, is depicted in Fig. XVIII-26. Although the resulting correlogram is hardly similar to the one shown in Fig. XVIII-20, its asymmetrical nature is, nonetheless, clearly apparent. An intuitive grasp of the underlying basis for this asymmetry can be gained from inspection of the three traces of Fig. XVIII-23. A comparison of the time course of the unit impulse responses of the tuned circuit with that of the lowpass filter indicates that, if the unit impulse response
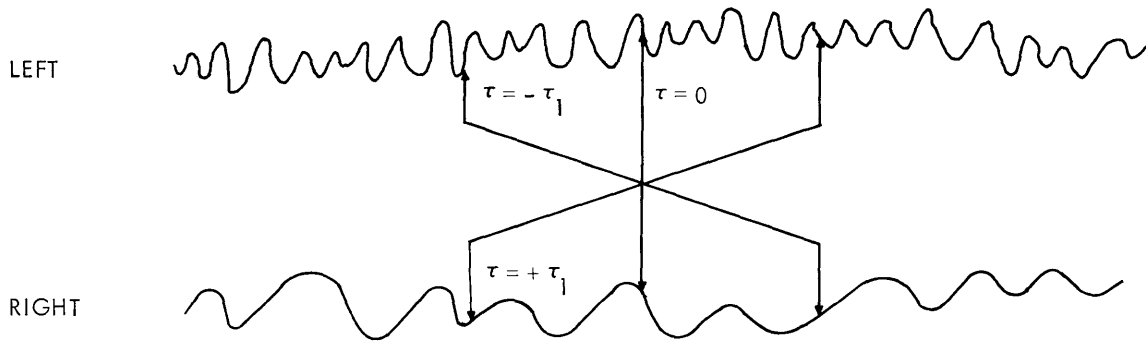
LEFT

$\tau = - \tau_1$ $\tau = 0$

$\tau = + \tau_1$

RIGHT

Fig. XVIII-22. Diagram illustrating comparison of EEG from the
left and right sides, for different delays.

Unit impulse responses

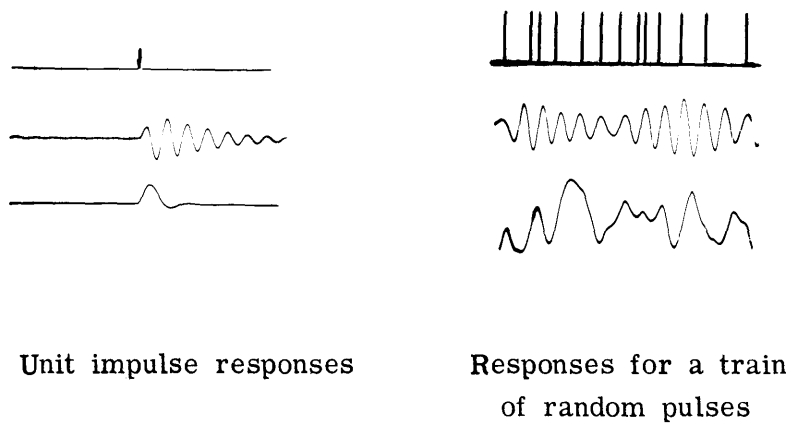Responses for a train
of random pulses

Fig. XVIII-23. Simulation of normal and abnormal EEG. The average interval
between successive pulses is approximately 3 msec. The fre-
quency of the tuned passive filter was 250 cps, and the cutoff
frequency of the lowpass filter was 150 cps.

RANDOM PULSE
GENERATOR 1

RANDOM PULSE
GENERATOR 2

RANDOM PULSE
GENERATOR 3

MIXING
CIRCUIT

MIXING
CIRCUIT
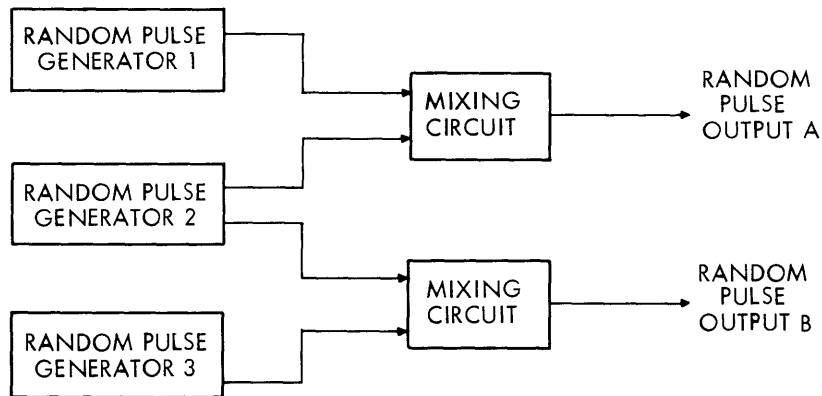
RANDOM
PULSE
OUTPUT A

RANDOM
PULSE
OUTPUT B

Fig. XVIII-24. Block diagram of arrangement for generation of 2 random
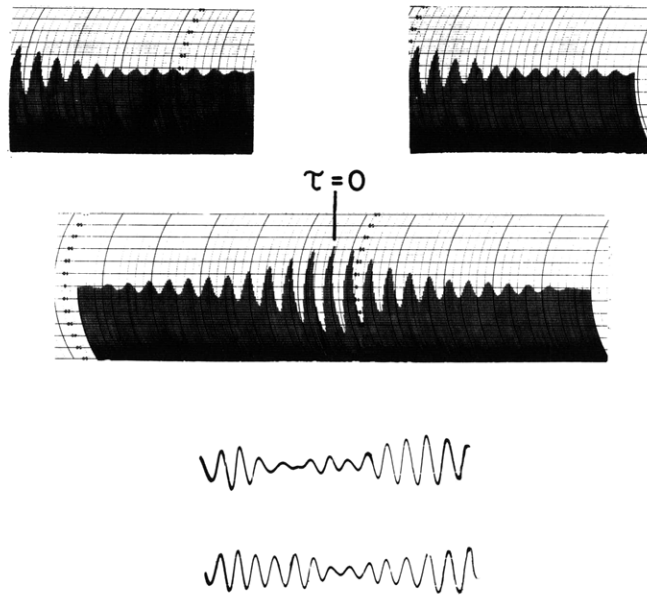pulse trains having a common component.

Fig. XVIII-25. Correlograms for simulated normal left and right occipital EEG.
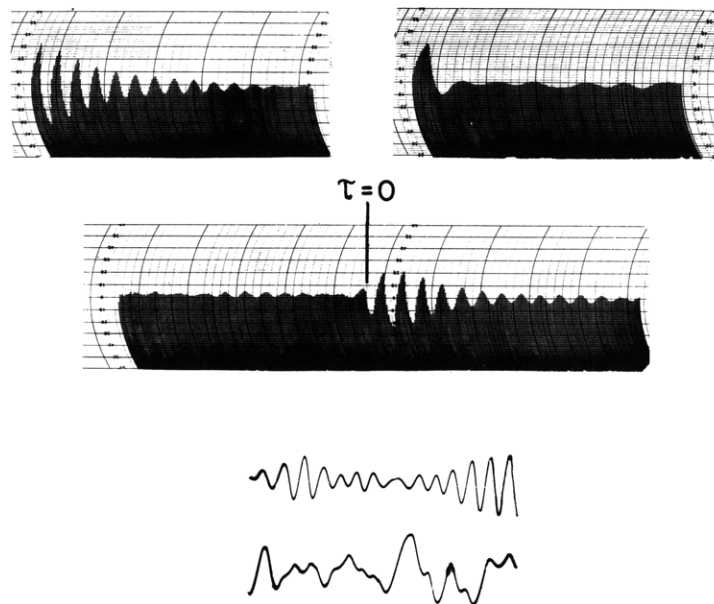

Fig. XVIII-26. Correlograms for simulated normal left and abnormal right occipital EEG.

of the lowpass filter is shifted to the left with respect to that of the tuned circuit, all correlation between the two would be rapidly lost as the displacement of the former to the left is successively increased. On the other hand, if the unit impulse response of the lowpass filter is shifted to the right with respect to that of the tuned circuit, the two will remain correlated to some degree (albeit to a decreasing extent) for a considerably greater time than would be the case for the shift to the left. It is just this asymmetry in correlation, with respect to positive and negative shifts in time, that is reflected in the crosscorrelogram shown in Fig. XVIII-26.

It should be emphasized that only one type of asymmetry was simulated in Fig. XVIII-26; neither the exact form of the asymmetry, nor the form of the cross-correlogram itself, illustrated in Fig. XVIII-20, is reproduced. Subsequent simulation experiments could include variation of types of unit impulse responses (Fig. XVIII-23) to simulate more closely the form of the asymmetrical correlogram in Fig. XVIII-20.

It is of interest in relation to the present results that the crosscorrelograms for pharmacologically induced unilateral slow-wave activity (Fig. XVIII-21) was of a symmetrical nature; this result could suggest that the pharmacologically induced slow-wave activity is more closely related to (or alternatively, is derived from) intrinsic activity of one cerebral hemisphere (e.g., if having as its analog the output of random pulse generator No. 1 or No. 3, in Fig. XVIII-24), whereas slow-wave activity appearing in the instance of structural pathology of the cerebral hemisphere may be more closely related to (or derived from) neuronal activity arriving at the cerebral hemispheres from midline structures, as discussed above. This suggestion is derived from the fact that random signals (in the present context, random slow waves in the EEG) do not correlate unless they are derived at least in part from a common source.[3]

Since the origin of the normal, as well as the abnormal, EEG is still a matter of considerable discussion, it is not possible to specify the exact nature of the physiological analogies of the simulation experiments described, but the relationship of cortical slow-wave activity and of the EEG to postsynaptic potentials that are derived in turn from nerve action potentials, as well as after-potentials of the latter,[4] obviously suggests itself as a possibility. It would be of interest to speculate about whether or not the time course of postsynaptic potentials might be increased under some circumstances if there is structural pathology of the cerebral cortex.

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References

1. J. S. Barlow and Margaret Z. Freeman, Comparison of EEG activity recorded from homologous locations on the scalp by means of autocorrelation and crosscorrelation analysis, Quarterly Progress Report No. 54, Research Laboratory of Electronics, M.I.T., July 15, 1959, pp. 173-180.

2. A Symposium on Dendrites, American Society of Electroencephalographers, Supplement No. 10, EEG Clin. Neurophysiol., November 1958.

3. J. S. Barlow, Autocorrelation and crosscorrelation analysis in electroencephalography, Trans. IRE, Vol. ME-6, pp. 179-183, 1959.

4. A. Fessard, Brain potentials and rhythms — Introduction, Handbook of Physiology, edited by J. Field (American Physiological Society, Washington, D.C., 1960), Section I (Neurophysiology) Vol. 1, Chapter 9, pp. 255-259.

E. TRANSISTORIZED CARDIAC TACHOMETER

This instrument is a portable, self-contained, heart-rate indicator. It is designed to operate with the following scales: 0-100, 0-200, and 0-400 beats per minute.

A block diagram of the instrument is shown in Fig. XVIII-27. Electrodes pick up the heart potential, which is amplified by a differential amplifier.[1] The advantage of the differential amplifier is that the potential between the electrodes (cardiac potential) can be greatly amplified while the common mode interference is attenuated. This allows the instrument to be used outside a shielded room. The output of the differential amplifier triggers a monostable multivibrator. The multivibrator is biased so that only the QRS complex of the electrocardiagram will trigger it.

The rectangular pulses from the multivibrator are led to a lowpass RC filter that has a 10-sec time constant. The output of the filter is proportional to the heart rate and has a small ripple at the frequency of the heart rate. The filter is followed by a difference amplifier that amplifies the output of the filter and also provides an electronic zero setting for the meter. The difference amplifier drives a microammeter that provides the read-out of the device. A circuit diagram of the tachometer is shown in Fig. XVIII-28.

When the instrument is in operation the ripple from the filter causes a pulsation of the meter pointer. When the heart rate is 70 beats per minute (a typical human pulse), the pulsation has a swing of ± 2 beats per minute about this value. This pulsation has proved to be a valuable indication when the user is adjusting the amplifier gain to give reliable triggering of the multivibrator. The pulsations do, however, limit the accuracy of the device to ± 3 per cent.

A switch (CT sig) and an input terminal (CT in) are provided for calibrating the instrument with a known pulse train. The unit may also be used as a low-noise differential amplifier for EKG potentials by connecting an oscilloscope or a pen recorder to the
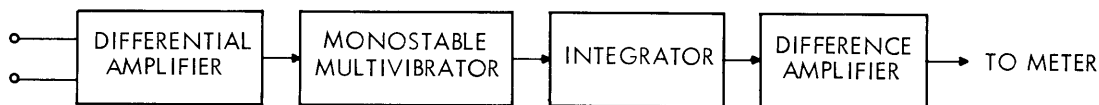

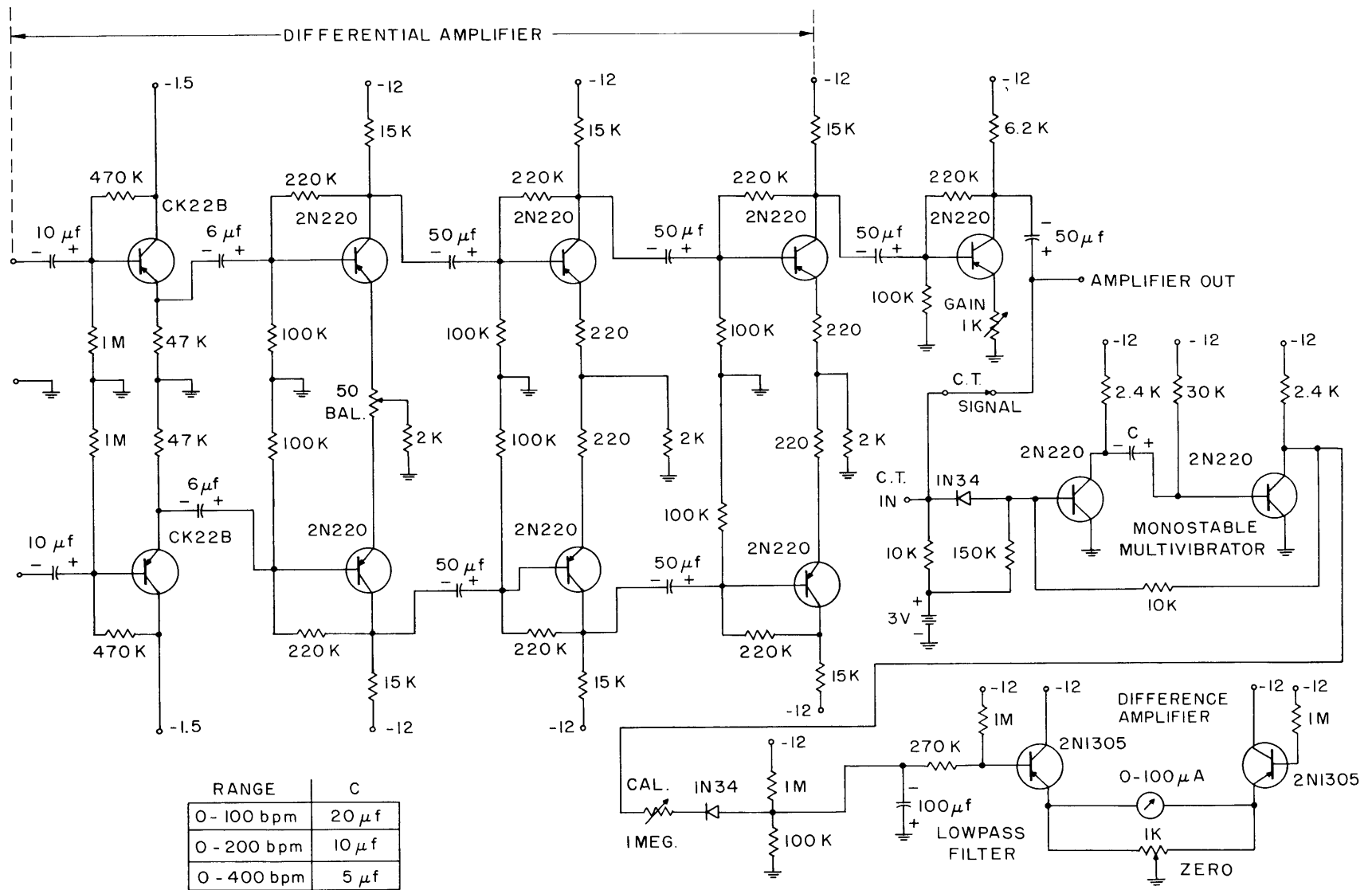Fig. XVIII-27. Block diagram of cardiac tachometer.

Fig. XVIII-28. Circuit diagram of cardiac tachometer.

RANGE	C
0 - 100 bpm	20 μf
0 - 200 bpm	10 μf
0 - 400 bpm	5 μf

output of the differential amplifier.

Thus far, the tachometer has been used successfully to measure human heart rate by means of electrodes taped to the skin and also to monitor heart rate of anesthetized animals by means of subdermal electrodes.

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References

1. R. T. Kado and W. R. Adey, A transistorized preamplifier for field study of EEG, Digest of the 1961 International Conference on Medical Electronics, New York City, July 1961, edited by Peter L. Frommer (The Conference Committee for the 1961 International Conference on Medical Electronics, Leslie E. Flory, Chairman, RCA Laboratories, Princeton, N.J., 1961) p. 172.